

Chapter 3: Ecological Needs of the Everglades

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Summary

The Everglades is an oligotrophic (nutrient poor) wetland that developed under conditions of severe phosphorus (P) limitation. In recent decades, increased P loading from human sources has caused several ecological changes indicative of cultural eutrophication. This chapter summarizes available research findings on the relationship between P enrichment and ecological change in the Everglades. These findings will help provide a scientific basis for identifying P concentrations and loads that do not cause an imbalance in natural populations of aquatic flora or fauna.

Reference Conditions of the Ecosystem

The predrainage or reference condition of the Everglades with regard to P is being reconstructed from written records, current conditions at least-impacted sites in the marsh interior, and paleoecological assessments. Historically, P inputs came largely from atmospheric deposition. Contemporary estimates indicate that the total P (TP) concentration in rainfall typically is less than ($<$) 10 $\mu\text{g/L}$ and that total atmospheric inputs (wet+dry deposition) average between 22 and 36 $\text{mg TP/m}^2/\text{yr}$. The Everglades also received periodic inflows of P-rich water from Lake Okeechobee (Lake), but these inputs likely were small relative to atmospheric inputs. Low historical P inputs are still reflected in the low P conditions in the Everglades interior. Water-column TP concentrations in interior areas are extremely low, averaging between 4 and 10 $\mu\text{g/L}$. Soil porewater P concentrations are consistently <50 $\mu\text{g/L}$ soluble reactive P (SRP) and often at or below 4 $\mu\text{g/L}$. Total P concentrations in surface soils range between 200 and 500 mg/kg and also are indicative of P limitation in this system.

Most natural populations of Everglades flora and fauna are adapted to conditions of low P. Soil microbes (bacteria, fungi and protozoa) regulate nutrient transformations that control P availability and ecosystem productivity. Periphyton (floating and attached algal mats) is abundant in oligotrophic areas and provides a habitat and a food source for invertebrates and fish. Periphyton also plays an important role in P storage, thereby maintaining low P availability in the marsh.

Sawgrass stands account for approximately 65 to 70% of the total vegetation cover in the oligotrophic Everglades. In many areas, these stands are interspersed with wet prairies, containing rushes and grasses, and deeper-water sloughs, containing water lilies and bladderwort. These habitats form a heterogeneous and dynamic landscape that is shaped by fluctuations in hydrology, fire, and other disturbances. Historically, cattail was a minor component of the Everglades flora and is believed to have occurred primarily in naturally enriched or disturbed locations. There is no evidence for the existence of dense cattail stands covering large areas in the predrainage Everglades as now occurs in parts of the northern Everglades.

With few exceptions (e.g., wading birds), less attention has focused on Everglades fauna than on the flora. Aquatic invertebrates such as insects, snails, and crayfish play important roles in the Everglades food web. Most invertebrates feed directly on periphyton and/or plant detritus and are, in turn, consumed by larger predators. Invertebrates are not distributed evenly among habitats and tend to be concentrated in periphyton-rich habitats such as sloughs, where food availability and dissolved oxygen (DO) concentrations are high. Fish are a key link between invertebrates and top predators such as wading birds, which historically were abundant in the Everglades. Fish biomass in oligotrophic areas of the Everglades is low relative to other wetlands, but becomes concentrated and available to predators when waters recede during the dry season.

Patterns of P Enrichment in the Marsh

For several decades, canal inflows have contributed P from agricultural runoff to many areas of the Everglades, with greatest inputs occurring in the northern Everglades. The penetration of canal P into different areas of the marsh varies as a function of inflow P loads and concentrations, as well as the direction of flow and elevation. Enrichment has been most extensive in Water Conservation Area (WCA) 2A, where elevated water-column TP concentrations have been detected as far as 7 km downstream of canal inflows. Intrusions of canal P into the Loxahatchee National Wildlife Refuge (Refuge) appear to be restricted to the marsh perimeter under current regulation schedules. The extent of P enrichment in WCA-3A has not been determined precisely, but water-column TP is elevated in areas adjacent to water-control structures and interior canals. Canal P inputs to Everglades National Park (the Park) are considerably lower than those entering the northern Everglades but still tend to be elevated compared with interior marsh locations.

Soil TP concentrations near canal inflows can be more than two-fold higher than those in the marsh interior. In WCA-2A, TP concentrations in surface soils downstream of canal inflows have increased over three-fold since the 1970s and may be continuing to increase as far as 7 km away from these inflows. Increased soil P in other areas (Holey Land, Rotenberger, and northern WCA-3A) appears to be a result of soil compaction and oxidation caused by overdrainage. Porewater P concentrations follow the same trends as those observed in soils, with concentrations in excess of 1,000 μg SRP/L soluble reactive P in highly enriched areas of the northern Everglades.

Ecological Responses to P Enrichment

Microbes and periphyton respond rapidly to P enrichment and, therefore, provide one of the earliest signs of eutrophication. Phosphorus enrichment is associated with increased microbial biomass and activity, resulting in faster rates of decomposition and nutrient cycling downstream of canal discharges. Accumulation of P by periphyton occurs quickly and results in accelerated photosynthesis, respiration, and a taxonomic shift towards species capable of faster growth under P-enriched conditions. Controlled dosing studies combined with sampling along marsh P gradients indicate that many of these changes occur at water-column TP concentrations in excess of approximately 10 $\mu\text{g}/\text{L}$ and that other nutrients such as N may become limiting to algal growth at TP concentrations near 30 $\mu\text{g}/\text{L}$. Increased macrophyte cover and density in enriched areas of the marsh reduce light penetration to levels that inhibit periphyton and submerged macrophyte growth. This decline in submerged productivity contributes to low water-column DO in P-enriched areas.

The growth of Everglades macrophytes generally is stimulated by increases in water and soil P concentrations. For example, sawgrass populations exhibit an increase in plant size, individual growth rates, and seed production along marsh P gradients. Several slough and wet prairie species also display positive responses to P enrichment at soil TP concentrations near 500 mg/kg. However, cattail has been shown to be a superior competitor to sawgrass and other Everglades macrophytes under P-enriched conditions. Consequently, enrichment proceeds with a decline in the coverage of sawgrass, sloughs, and wet prairies as these habitats gradually are replaced by cattail. This transition occurs more slowly than for periphyton and current models suggest multi-year time lags between P enrichment and vegetation change.

Whereas cattail was uncommon in the predrainage Everglades, dense stands of this species have expanded rapidly in recent decades. In the northern Everglades, this species commonly is associated with P-enriched canal inflows. Cattail expansion also has occurred in areas of the central Everglades where existing soil P has been concentrated as a result of overdrainage. Cattail invasion rarely has been documented in field enrichment experiments. However, experimental studies may not span a sufficient timeframe given the potential for substantial time lags as already mentioned. Cattail invasion may be limited by several factors, including reduced seed viability following dispersal and poor seedling growth and survival, particularly in flooded and low-nutrient soils. Thus, while established cattail stands are extremely tolerant of a wide range of environmental conditions, successful colonization of new locations appears dependent upon favorable environmental conditions near the time of seed dispersal.

Invertebrates and other aquatic fauna are affected by P-induced changes in the periphyton and macrophyte food base and declines in water-column DO. Phosphorus enrichment of specific habitats (e.g., sloughs) may increase invertebrate densities and diversity. However, invertebrate abundance tends to be low in emergent macrophyte stands, which cover much of the marsh in enriched areas. Consistent with the loss of periphyton-rich habitats in response to P enrichment, invertebrate assemblages in enriched areas are dominated by species that are tolerant of low DO and that rely on cattail detritus rather than periphyton as a primary food source. Available evidence indicates that fish are more abundant in enriched areas of the marsh, although accurate measurements in cattail habitats have been difficult to obtain. Nutrient enrichment can affect bird communities indirectly either through effects on their food or through effects on vegetation structure, which provides foraging and nesting substrate. An analysis of wading bird abundance in relation to vegetation in the northern Everglades indicated that the abundance of several species is higher in areas with moderate cattail cover, but is lower in dense cattail habitats.

Modeling the Effects of Enrichment

Effects of P enrichment on the Everglades are being investigated using models with varying levels of ecological and computational complexity. All of the models discussed below were developed by the District unless otherwise noted, and address the relationship between nutrient loading and resulting water quality (Act 4(e)3) and biological responses.

The Everglades Water Quality Model (EWQM) evaluates the relationship between P loads and concentrations in the Everglades Protection Area. Model results indicate that P loads from the Everglades Agricultural Area have a significant effect on water-column P concentrations in areas downstream of inflow structures and canals. The model also shows that decreasing P loads from the Everglades Agricultural Area can directly reduce P inputs to the Park.

The Everglades Phosphorus and Hydrology (EPH) model was developed by Tetra Tech, Inc. for the Sugar Cane Cooperative of Florida and, like the EWQM, evaluates the relationship between P loads and concentrations in the Everglades Protection Area. The EPH model was used to evaluate three scenarios: the base case (no P reductions), the Act case (includes operation of six Stormwater Treatment Areas [STAs] and P reductions of 25% by on-farm Best Management Practices) and a modified Act case where one of the STAs (number 3/4) is removed, and BMPs are assumed to reduce P loads by 50%. Under the Act and modified Act case, the EPH model predicts decreased P concentrations in areas near discharges from the Everglades Agricultural Area, but, unlike EWQM results, predicts little impact on P concentrations entering the Park.

The SAWCAT model (Wu et al., 1997), a probability model developed to understand the impact of soil P on cattail invasion in WCA-2A, found that the probabilities of sawgrass changing to cattail between 1973 and 1991 were most dependent upon the proximity of existing cattail stands and the spatial pattern of soil TP. A logistic function, built from spatial correlations of soil TP (DeBusk et al., 1994) and cattail distributions in WCA-2A (Jensen et al., 1995), estimated that the threshold for accelerated cattail invasion was ~650 mg/kg soil TP.

The Everglades Phosphorus Gradient Model (EPGM), was developed by outside consultants for the U.S. Government to provide generalized predictions of the effects of P loads on receiving water and soil P concentrations and resulting growth of cattail communities. The District used the EPGM to determine if implementing the hydropattern restoration features of STAs would change soil P concentrations to a degree that would affect cattail distributions in the WCAs.

The Everglades Landscape Vegetation Model (ELVM) predicts vegetation succession based on macrophyte growth and responses to disturbances, hydrology, and nutrients. Preliminary results of this model applied to WCA-2A predict that soil P concentrations in areas most affected by canal P have increased sufficiently to support cattail expansion for as long as 20 years, even if existing inputs are curtailed completely.

The Everglades Landscape Model (ELM) predicts long-term, regional effects of water and nutrient management scenarios on vegetation. This model simulates interactions among hydrology, nutrients, and macrophytes across the entire EPA and Big Cypress Preserve. As for the ELVM, the ELM suggests periphyton enriched areas of WCA-2A will remain so for several years following load reductions and that recovery of native periphyton assemblages will be hindered by high macrophyte biomass in these areas.

Conclusions

The Everglades ecosystem developed under conditions of extreme P limitation, and it is clear that anthropogenic P loads have altered this unique resource. Available evidence indicates that the ecological changes caused by enrichment manifest themselves over different time scales, but generally occur within a fairly narrow range of water-column TP concentrations between roughly 10 and 30 $\mu\text{g/L}$. This response range is similar to those established previously for other types of freshwater ecosystems.

Current studies are focusing on spatial and temporal variation in ecosystem responses to P enrichment and the rate of recovery following reductions in P inputs. For example, a largely untested hypothesis is that different habitats vary in their sensitivity to P enrichment. It also is unclear how the rate and extent of ecosystem change is affected by the level of P enrichment. Finally, interactions between P

enrichment and other factors such as hydrology and fire must be understood in order to predict ecological responses to management actions that involve both water quality and hydrologic restoration.

Evidence from other ecosystems suggests that the rate at which the Everglades ecosystem recovers from eutrophication will be considerably slower than the initial enrichment process. Additional research is planned or ongoing to understand the process of ecosystem recovery following P load reductions so as to develop realistic timeframes and expectations for restoration. This work will focus on determining expected rates of marsh recovery following reduced P inputs, including reductions in water-column and soil P concentrations, the potential for the continued spread or recession of cattail, and the rate of ecological recovery anticipated for areas already altered by P enrichment.

Introduction

Defining the “Ecological needs of the Everglades” requires consideration of several factors including hydrology, nutrients such as phosphorus (P), other water quality issues (e.g., mercury, pesticides), and the spatial extent of habitats required to support self-sustaining populations of native fauna, including invertebrates, wading birds, deer, and panther. For the purposes of this Interim Report, ecological needs will be defined primarily in terms of P (this chapter) and hydrology (**Chapter 2**). These chapters, in turn, correspond to Project RAM-6 (Interpret Class III Phosphorus Criterion Research) and RAM 10 (Hydrologic Needs of the Ecosystem) of the State's Everglades Program Implementation Program Management Plan (SFWMD & DEP, 1997; **Chapter 1**). Other water quality issues are discussed in **Chapter 4** (Water Quality of the Everglades Protection Area) and **Chapter 7** (The Everglades Mercury Problem).

Phosphorus is a key element controlling aquatic productivity, and the widespread use of this nutrient to increase soil fertility is responsible for the eutrophication of freshwater ecosystems worldwide (Tiessen, 1995). The ecological effects of increased P loading on lakes and rivers have been well-documented and include excessive productivity, reduced dissolved oxygen, changes in species composition, and reduced biodiversity (National Academy of Sciences, 1969; Likens, 1972; Havens & Steinman, 1995). The relationship between increased P loading and wetland change has not been widely investigated because most attention has focused on the ability of wetlands to transform and remove pollutants rather than on the ecological changes associated with this removal process (e.g., Howard-Williams, 1985; Moshiri, 1993; Olson, 1993). The need for national water quality standards for wetlands has been recognized (USEPA, 1990) in an effort to afford these systems the same level of protection currently provided to other water bodies. Several states have begun developing water quality standards to protect designated uses of wetlands (USEPA, 1996).

The Everglades ecosystem (**Figure 3-1**) developed under extremely low rates of P supply. Increased rates of P loading from agricultural and urban sources over the past several decades have been associated with changes in ecological conditions that are indicative of cultural eutrophication. In response to this eutrophication, the Everglades Forever Act (Act) was passed to enhance and protect the Everglades. The Act mandates, among other things, that research, monitoring, and modeling be conducted to guide nutrient management decisions affecting the Everglades/Florida Bay system. Accordingly, joint SFWMD-DEP research programs were initiated to determine P concentrations and loads that will maintain pristine Everglades conditions. Substantial efforts also have been initiated by Duke University Wetlands Center,

University of Florida, Florida International University, the United States Geological Survey, and the Environmental Protection Agency to study various aspects of the P problem. Specifically, the Act calls for the development of a numeric water quality criterion for P that will “prevent an imbalance in the natural populations of aquatic flora or fauna and to provide a net improvement in the areas already impacted.” Data including those discussed herein will be used in rulemaking by the state's Environmental Regulatory Commission (ERC) to set such a criterion for the Everglades. The process of P criterion development being pursued by DEP is outlined in **Appendix 3-1**.

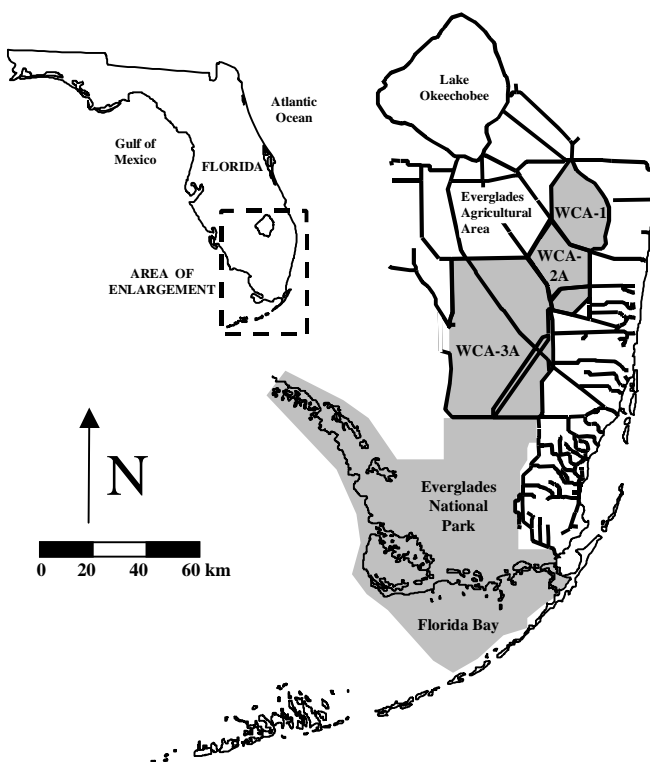


Figure 3-1. Major hydrologic units of the remnant Everglades-Florida Bay ecosystem (shaded areas). The canal and levee system is represented as solid black lines; see **Chapter 1** for additional information.

The objective of this chapter is to summarize data and findings as interim progress toward:

- Defining reference (predrainage) conditions for P in the Everglades;
- Documenting the ecological impacts caused by increased P inputs; and
- Identifying critical P concentrations and loads that cause changes in flora or fauna.

This summary is based primarily on two sources of information: (1) manuscripts published in the peer-reviewed literature; and (2) widely distributed reports containing otherwise unpublished findings. Written requests for all available manuscripts, reports, and unpublished data were sent to each of the research groups listed above and relevant information received has been included in this report. The findings and conclusions reported here should be considered interim pending the final results of ongoing studies by several research groups.

Reference Conditions of the Ecosystem

Defining predrainage or reference conditions of the Everglades is a critical first step in determining the extent of P enrichment and associated ecological impacts. Reconstructions of reference

conditions are based on: (1) written historical records; (2) sampling in least-impacted locations (i.e., reference sites) that are believed to best portray historical conditions in different regions and habitats; and (3) paleoecological assessments, which entail the collection and dating of soil cores and the analysis of nutrient content and preserved materials (e.g., pollen, algal cell walls, charcoal) that are diagnostic of past conditions and events. Unfortunately, historical descriptions of the system are scarce, and most are qualitative and lack critical detail. While historical descriptions of large-scale vegetation patterns are relatively complete (e.g., Davis, 1943; Loveless, 1959), information on historical water quality conditions are sparse prior to the 1970s. Paleoecological assessments can provide quantitative information on past changes in nutrient conditions but are limited by the extent of preservation of diagnostic materials. Relatively little paleoecological evidence is currently available and, therefore, much of what is known about the ecological characteristics of the predrainage Everglades is based on relatively recent data from reference sites in the marsh interior.

Water Quality

Phosphorus Loading

Nutrient inputs to the Everglades are derived primarily from atmospheric deposition (rainfall and dry fallout), which is typically low in P in remote areas. Estimates of annual atmospheric P inputs in south Florida and reconstructions of P accumulation in Everglades soils (see below) indicate that historical loading rates were extremely low, probably averaging well below 100 mg TP/m²/yr (SFWMD, 1992; SFWMD, 1997). As discussed below, these historical rates are still reflected in the low concentrations of P in the surface water and soils and the species composition of periphyton and vegetation in interior areas of the Everglades that are far removed from anthropogenic P inputs.

The accuracy of atmospheric P loading estimates is limited by the ability to obtain uncontaminated samples of rainfall and dry fallout (SFWMD, 1997). Contemporary measurements of P concentrations in rainfall and dryfall (e.g. Waller & Earle, 1975; Davis, 1994) reflect regional agricultural and urban sources as well as background inputs and, consequently, overestimate historical inputs. These measurements typically are conducted using ground-based collection systems, which are susceptible to contamination from local P sources (e.g., guano, insects) that do not represent new inputs of P to the ecosystem. Additionally, previous analyses of these data have relied on statistical procedures that are affected unduly by contaminated samples.

Rainfall samples collected at the District atmospheric deposition collection stations (**Figure 3-2**) illustrate the problems associated with the collection and analysis of atmospheric deposition data. Phosphorus concentrations vary greatly, even among samples collected at the same station, and the data are highly skewed due to a small number of extremely high values that are likely caused by contamination. Most samples contain TP in concentrations near or below the limits of analytical detection (4 µg/L); thus, the low end of the distribution is truncated and cannot be measured precisely. Average rainfall TP concentrations have been estimated previously from these types of data sets by calculating the arithmetic mean concentration (e.g., Waller & Earle, 1975). This statistic is inappropriate for data with the properties just described and consistently overestimates the central tendency of the data, sometimes by a wide margin. The median P concentration, a more appropriate estimator of the average value, ranges between 4 and 7 µg/L across all the District collection stations whereas mean concentrations are consistently higher and considerably more variable (**Figure 3-2**). Using a different statistical approach, Ahn (1998) also concluded that TP concentrations in rainfall across the Everglades are consistently below 10 µg/L.

Similarly, independent estimates of rainfall TP across Florida have found median concentrations to range between 5 and 7 $\mu\text{g/L}$ (Brezonik et al., 1982; Pollman & Landing, 1997).

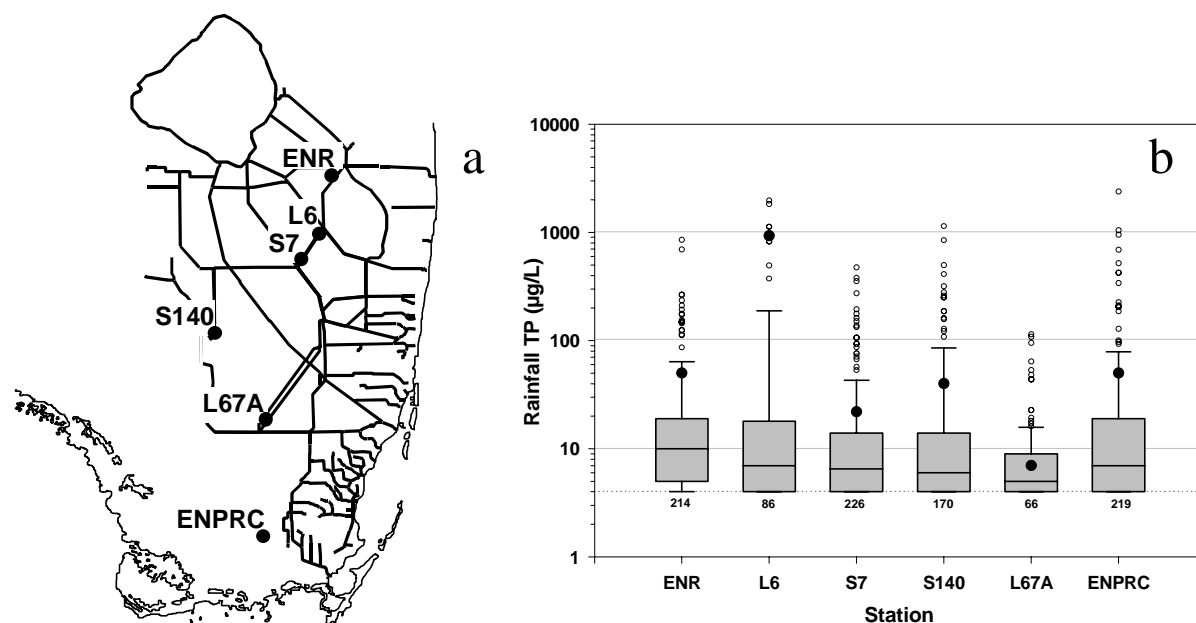


Figure 3-2. a. District atmospheric deposition collection stations. b. Range of TP concentrations in rainfall samples collected from these stations throughout the Everglades between 1987 and 1997. The top, mid-line, and bottom of each box represents the 75th, 50th (median), and 25th percentiles of data, respectively; the vertical lines represent the 10th and 90th percentiles; large closed circle is the arithmetic mean; small open circles are observations outside the 90th percentiles. Numbers below each box are the number of samples collected at that site. Dashed line represents the analytical detection limit for TP (4 $\mu\text{g/L}$); concentrations at or below the detection limit were analyzed as 4 $\mu\text{g/L}$.

Dryfall is believed to account for much of the atmospheric P inputs to the Everglades. However, as for rainfall, accurate measurement of dry deposition rates is confounded by contamination from local and regional sources (SFWMD, 1997) and likely overestimates historical P deposition rates. Available information on wet and dry deposition obtained from the District atmospheric deposition collection stations (see Ahn and James in review for sampling and analysis methods) illustrates the range and relative magnitude of these P inputs for locations across the Everglades (**Figure 3-3**). Both wet and dry deposition rates varied markedly among sampling events; however, mean dry deposition rates exceeded wet deposition at all but one site (S7) and accounted for between 44 and 80% of total TP deposition (mean for all sites = 64%). These measurements yield mean and median total deposition rates of 36.5 and 21.9 $\text{mg TP/m}^2/\text{yr}$, respectively, which are similar to independent estimates obtained for south Florida (Landing, 1997).

Atmospheric inputs of P to the predrainage Everglades were augmented by inflows from Lake Okeechobee. The Lake was connected by surface-water flows to the northern Everglades during periods of

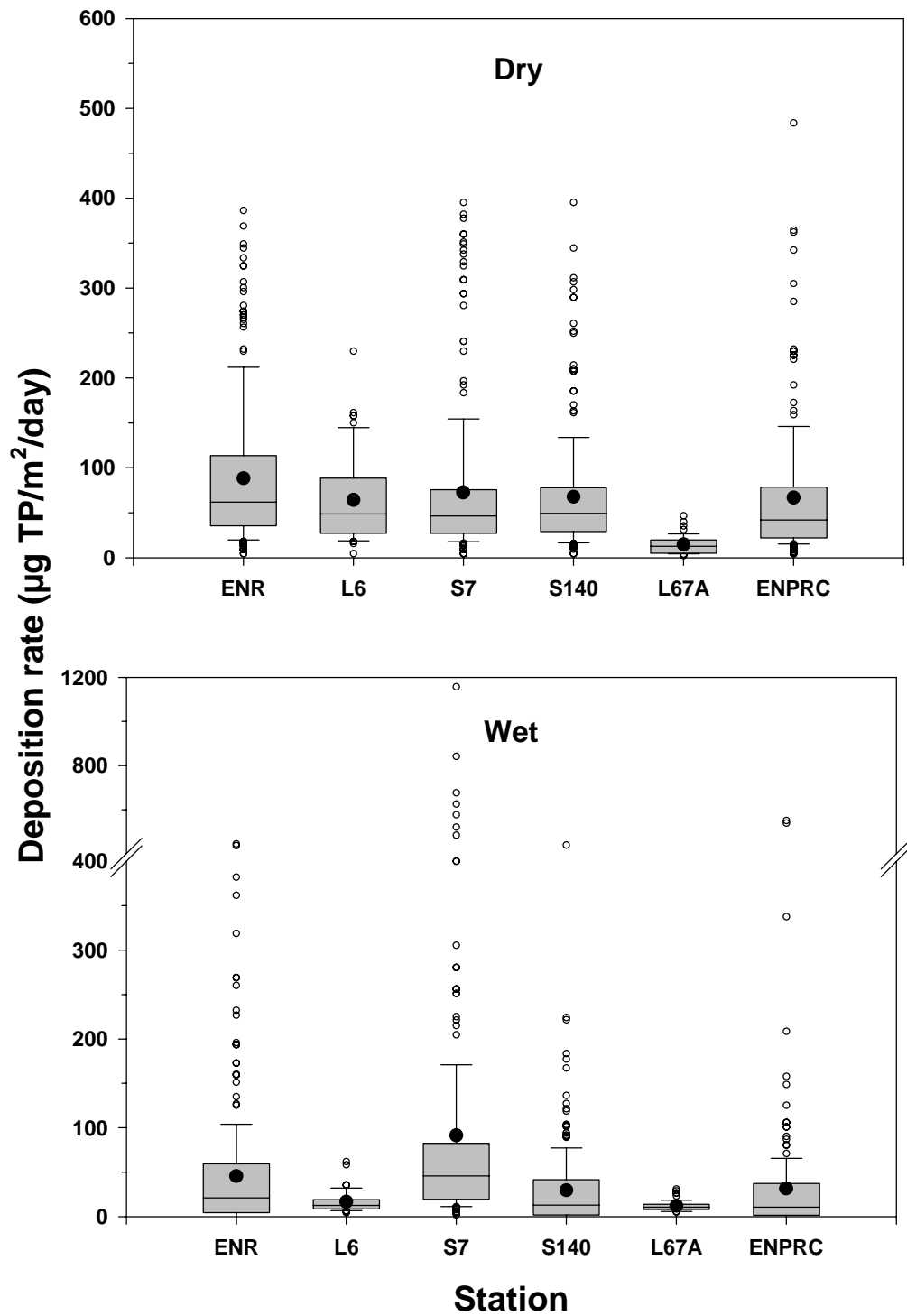


Figure 3-3. Wet and dry deposition samples collected from the District atmospheric deposition collection stations throughout the Everglades between 1992 and 1996. See **Figure 3-2** for interpretation of box plots.

high water (Parker et al., 1955). Paleoecological evidence indicates that Lake Okeechobee has been eutrophic for several thousand years (Gleason & Stone, 1975), suggesting that inflows of lake waters probably were enriched in P compared with the marsh. The amount of P supplied to the predrainage Everglades from Lake inflows is not known; however, contemporary measurements of soil P indicate historically enriched conditions within a zone of custard apple (*Annona glabra*) and sawgrass (*Cladium jamaicense*) south of the Lake (Snyder & Davidson, 1994). Given the proportion of historical hydrologic inputs from rainfall (>90%) and Lake Okeechobee (<10%) (SFWMD, 1998), it is likely that effects of Lake inflows on Everglades P dynamics were limited to northernmost areas of the marsh.

Water-column P concentrations

Interior areas of the Everglades generally retain the oligotrophic characteristics of the predrainage ecosystem, and provide the best contemporary information on historical P concentrations. Available water-column TP data are summarized for several interior sampling stations that are far from canal inflows, and are believed to best reflect the reference condition for nutrients in different areas of the marsh (**Figure 3-4**). These data likely represent an upper estimate of historical TP concentrations in the Everglades since several stations are located in areas that either have been: (1) excessively drained (e.g., northern WCA-3A), a condition which promotes soil oxidation and P release; or (2) so heavily exposed to canal inflows (e.g., WCA-2A) that some P inputs likely have intruded even into interior areas.

Median water-column TP concentrations at these reference stations range between 4 and 10 $\mu\text{g/L}$ throughout these areas and are lowest in southern areas of the marsh (e.g., Taylor Slough and the C-111 basin), which have been least affected by anthropogenic nutrient loads. Mean concentrations are more variable among stations (exceeding 10 $\mu\text{g/L}$ in some areas) largely as a result of periodic concentration excursions during periods of low water and/or marsh drying. High P concentrations at reference stations can be attributed to P released as a result of oxidation of exposed soils (Swift & Nicholas, 1987), increased fire frequency during droughts (Forthman, 1973), and difficulties in collecting water samples that are not contaminated by flocculent marsh sediments when water depths are low. Localized enrichment in the pristine Everglades also is associated with bird rookeries, alligator holes and other areas of natural disturbance (Davis, 1994). However, it is important to recognize that these forms of enrichment (e.g., soil oxidation, fecal inputs) represent recycling of existing P and do not affect the total amount of P stored in the marsh.

Other key water chemistry features

Interior areas of the Everglades differ with respect to pH and concentrations of major ions such as bicarbonate, calcium, and sodium. Surface waters across much of the Everglades including WCA-2A, WCA-3A, and Everglades National Park (Park) are slightly basic and highly mineralized (i.e., high ionic content). In contrast, the interior of the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Refuge) is slightly acidic and contains extremely low concentrations of major ions, a condition which reflects the rainfall-driven hydrology of this area. These background differences among Everglades marshes influence species composition (e.g., Swift & Nicholas, 1987) as well as the water quality and biological impacts caused by canal inflows (e.g., Gleason et al., 1975).

Water-column concentrations of total nitrogen (TN) (1000 to 2500 $\mu\text{g/L}$) and other macronutrients are relatively high in interior areas compared with those for P (generally <10 $\mu\text{g/L}$). Ratios of TN:TP at reference sites generally exceed 100:1 weight:weight and are indicative of strong P rather than N limitation

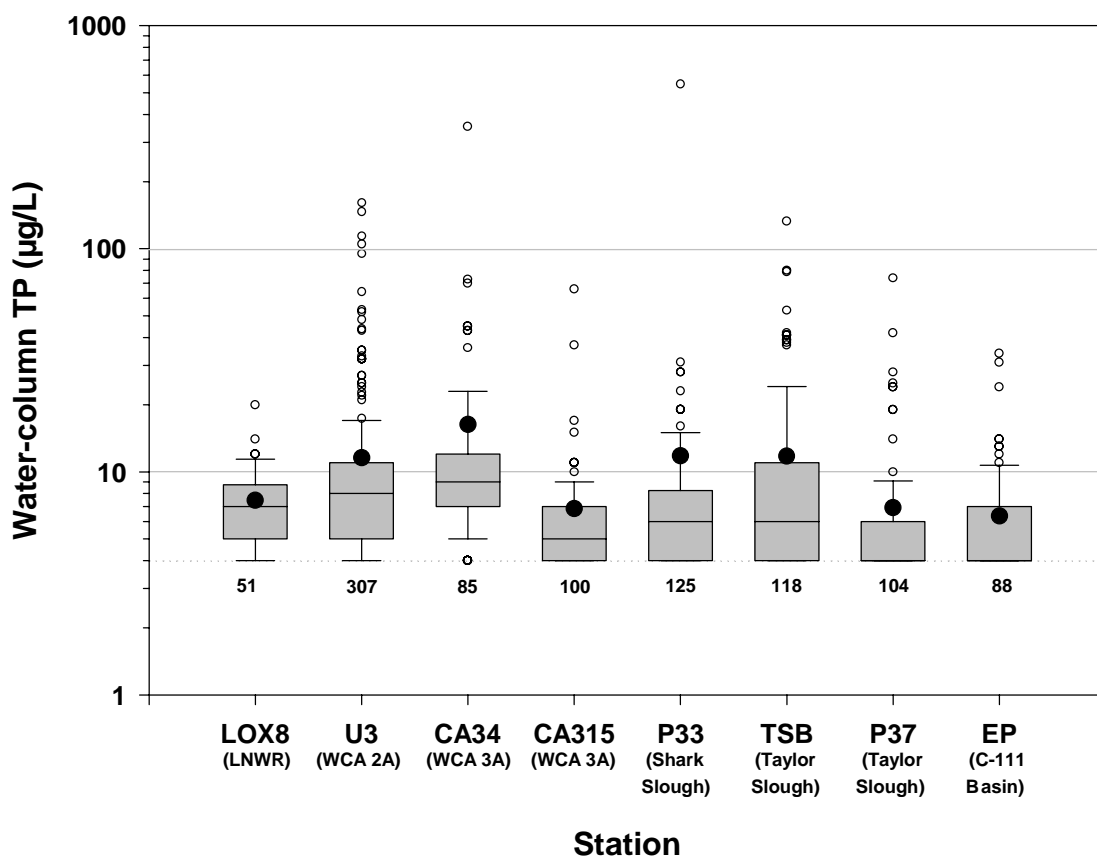


Figure 3-4. Range of TP concentrations in surface water samples collected from interior marsh sampling stations (see **Figures 3-8, 3-10, 3-11, and 3-12** for locations).

(Swift & Nicholas, 1987; McCormick et al., 1996). Concentrations of micronutrients (e.g., copper, iron, silica, and zinc) vary but generally are not considered limiting compared with the extremely low P concentrations in the marsh interior.

Oxygen is an absolute requirement for aerobic aquatic organisms, and changes in dissolved oxygen (DO) concentrations can play an important role in determining population distributions and rates of ecological processes in aquatic ecosystems. Interior Everglades habitats exhibit characteristic diel (24-hour) fluctuations in water-column DO, although aerobic conditions are generally maintained throughout much or all of the diel cycle (Belanger et al., 1989; McCormick et al., 1997). High daytime concentrations in open-water habitats (i.e., sloughs, wet prairies) are a product of photosynthesis by periphyton and other submerged vegetation. These habitats may serve as oxygen sources for adjacent sawgrass stands, where submerged productivity is low (Belanger et al., 1989). Oxygen concentrations decline rapidly during the night due to periphyton and sediment microbial respiration, and generally fall below the 5 mg/L standard for Class III Florida waters (Criterion 17-302.560(21), F.A.C.). However, these diurnal excursions are characteristic of reference areas throughout the Everglades (McCormick et al., 1997) and are not considered a violation of the Class III standard (Nearhoof, 1992). See **Chapter 4** of this Report for additional discussion of the applicability of State DO standards to Everglades marshes.

Soil and Porewater

In the early 1900s the Everglades organic soils were categorized into three groups based on the overlying vegetation (Baldwin & Hawker, 1915). Soils close to Lake Okeechobee were classified as custard apple muck, based on the dominance of custard apple. Further away from the lake, land was dominated by willow (*Salix* spp) and elderberry (*Sambucus canadensis*), and the soils were classified as willow and elder soils. However, the predominant organic soil in the Everglades was sawgrass peat, with sawgrass as the dominant vegetation. Of these various soil types, custard apple soils were considered to have a greater native fertility than sawgrass soil that formed under low-nutrient conditions (Snyder & Davidson, 1994). By the late 1940s, extensive soil surveys were completed (Davis, 1946; Jones, 1948), and the peat soils of the Everglades were classified into two main groups: Everglades peat (derived mostly from sawgrass) and Loxahatchee peat (derived primarily from slough species such as water lily).

Although the majority of soils data collected in the early 1900s were descriptive, there were a few accounts of soil samples collected and analyzed for nutrients. An examination of these records showed that at sites adjacent to Lake Okeechobee, P concentrations in the upper 30 cm of organic soil averaged 0.42 to 0.48% P_2O_5 (1,800 to 2,000 mg P/kg) (Hammar, 1929). In contrast, at sites near Tamiami trail, representative of the Everglades interior, P concentrations averaged 0.1% P_2O_5 (~400 mg P/kg) in muck, marl and hammock areas (King, 1917). Caution should be used when comparing nutrient data collected in the early 1900s versus that collected today, because modern analytical techniques are likely more accurate and precise.

Present-day soil nutrient data also may be used to estimate reference conditions by evaluating nutrient concentrations in areas that are outside the zone of nutrient impact. Total P concentrations in the surface 0-10 cm of soil in interior areas of the Holey Land Wildlife Management Area, WCAs and Rotenberger Wildlife Management Area range between 200 and 500 mg/kg (DeBusk et al., 1994; Reddy et al., 1994a; Newman et al., 1997; Richardson et al. 1997; Newman et al., 1998; USEPA, 1998). In the Park, soil TP concentrations downstream of canal inflows ranged from 1,420 mg/kg near the inflows to as low as 320 mg/kg farther downstream (Doren et al., 1997), suggesting that background TP concentrations for the Park were < 400 mg/kg.

In addition to variations in nutrient concentration per soil mass (mg/kg), nutrient content of the soils also changes per unit volume as a function of changing soil bulk density. The typical bulk density of flooded Everglades peat soils is approximately 0.08 g/cm³, whereas soils subjected to extended dry out and oxidation can have bulk densities greater than 0.2 g/cm³ (Newman et al., 1998; USEPA, 1998). Studies in other wetlands have shown that plant growth increases linearly with increases in bulk density from 0.1 to 0.4 g/cm³ (DeLaune et al., 1979; Barko & Smart, 1986). Thus, the expression of soil nutrient data on a volumetric (bulk-density-corrected) basis may provide greater information relative to plant growth. Following correction for the varying bulk densities in the peat soils of the Everglades, a historical TP concentration of < 40 µg/cm³ may be applicable for most regions (DeBusk et al., 1994; Reddy et al., 1994a; Newman et al., 1997; Newman et al., 1998; Reddy et al., 1998). In the Refuge, most of the interior area is encompassed within 20 µg TP/cm³ (Newman et al., 1997).

Porewater samples generally are collected at the same sites where soil coring is performed. These data show that the surface 0-10 cm soil porewater collected from interior areas of the marsh typically has SRP concentrations of < 50 µg/L and, frequently, these values are at or below analytical limits of detection

(4 µg/L) (DeBusk et al., 1994; Koch-Rose et al., 1994; Reddy et al., 1994a; Vaithyanathan & Richardson, 1995; Newman et al., 1997; Reddy et al., 1998).

Soil Microbes and Biogeochemical Cycles

Wetlands host complex microbial communities including bacteria, fungi, protozoa, and viruses. The size and diversity of microbial communities are related directly to the quality and quantity of the resources (i.e., nutrients, energy sources) available in the system. Microbial biomass and activity is highest in habitats where these resources are concentrated, including periphyton mats, plant litter, and surface soils. Microbial processes regulate major nutrient cycles in wetlands, and play an important role in determining water quality and ecosystem productivity.

Unlike carbon (C) and nitrogen (N), P added to wetlands accumulates within the system, because there is no significant gaseous loss mechanism in the P cycle. Steady, external P loading to oligotrophic wetlands such as the Everglades results in a transformation from a P-limited to a P-enriched system. Microbial communities respond to this enrichment with increased biomass and accelerated rates of various processes regulated by microbes. Because of the short life cycles of microbes, they respond rapidly to any changes in nutrient or energy source status of wetlands, and thus provide an early warning signal of eutrophication.

Microbial populations regulate rates of organic matter decomposition, the process whereby nutrients are recycled within all ecosystems. Decomposition rates are influenced by a number of factors including the quality of organic substrates (DeBusk & Reddy, 1998), hydroperiod (Happel & Chanton, 1993), the supply of electron acceptors (D'Angelo & Reddy, 1994a, b), and the addition of growth-limiting nutrients (McKinly & Vestal, 1992; Amador & Jones, 1995). Fluctuations in water depth create alternating aerobic and anaerobic conditions, which may stimulate organic matter decomposition and nutrient release (Reddy & Patrick, 1975). However, N and P release during decomposition and the resulting concentration in the porewater are influenced strongly by soil physico-chemical properties and the C:N:P ratios of the decomposing plant detritus and soil organic matter (Webster & Benfield, 1986; Enriquez et al., 1993).

Wetlands are characterized by both aerobic and anaerobic zones in the water-column, periphyton and litter layers, surface soils, and the root zone of aquatic macrophytes. The juxtaposition of aerobic and anaerobic zones support a wide range of microbial populations and associated processes mediated by microbes. Aerobic populations are restricted to periphyton mats in the water-column, the plant detritus layer, and the top few mm of the surface soil, while anaerobic populations dominate most of the soil profile as well as anoxic microsites in other habitats.

Oxygen concentrations in the detrital layer and attached periphyton mats vary on a diel basis as a result of photosynthesis during daylight hours (**Figure 3-5**). In addition, macrophyte transport of oxygen to the root zone also supports aerobic populations in the rhizosphere. Anaerobic bacteria can use alternative terminal electron acceptors such as nitrate, sulfate, and carbon dioxide to support their respiration. Anaerobic activity in the Everglades is dominated by methanogenesis, where microbes utilize HCO_3^- and organic substrate to produce methane.

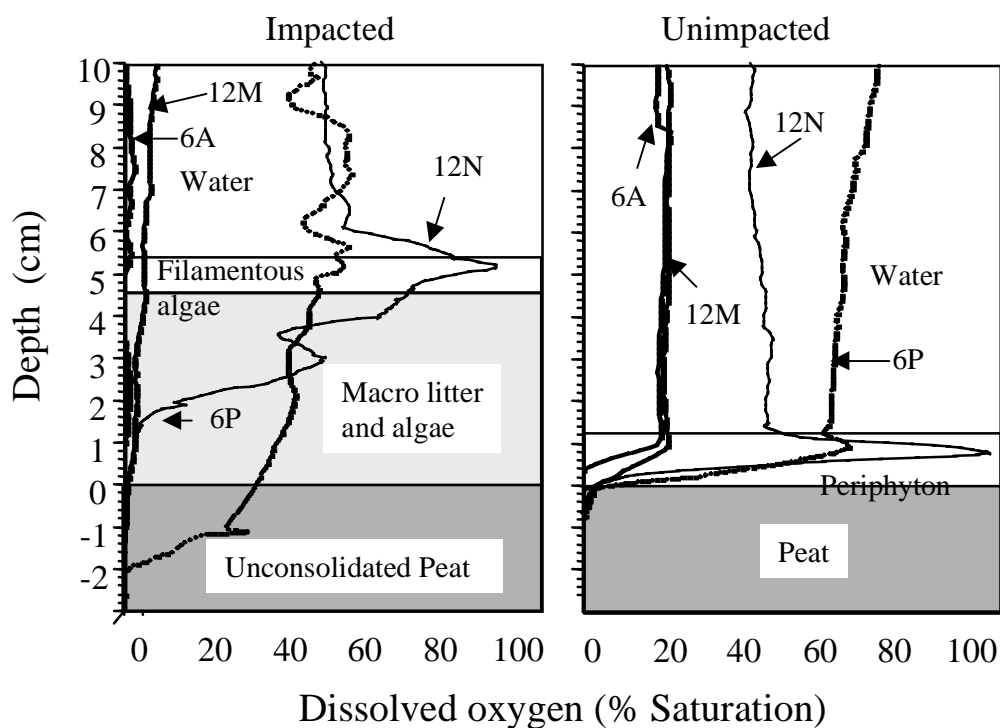


Figure 3-5. Vertical oxygen profiles with depth in the water-column, periphyton, and soil layers at nutrient-impacted and unimpacted sites. Individual lines show percent saturation at 6:00 a.m. (6A), noon (12N), 6 p.m. (6P), and midnight (12M).

Periphyton

Aquatic vegetation and other submerged surfaces in wetlands are covered with a community of algae, bacteria, and other microorganisms referred to as periphyton. Periphyton exhibits three growth forms: (1) benthic (growing on the soil surface); (2) epiphytic (growing attached to rooted vegetation; and (3) floating (growing on the water surface, sometimes in association with other floating vegetation such as *Utricularia purpurea*). All three forms of periphyton are abundant in oligotrophic areas of the Everglades and account for a significant portion of marsh primary productivity. Periphyton represents an important habitat for invertebrate populations and, along with macrophyte detritus, forms the base of the Everglades food web (Browder et al., 1994; Rader, 1994). These mats account for much of the P storage in open-water habitats and play a critical role in maintaining low P concentrations in reference areas of the marsh (McCormick et al., 1998; McCormick & Scinto, in press).

Periphyton abundance and productivity exhibit predictable spatial and seasonal patterns in the oligotrophic Everglades. Periphyton typically accounts for much of the vegetative biomass and primary productivity in sloughs and wet prairies (Wood & Maynard, 1974; Browder et al., 1982; McCormick et al., 1998), and open-water habitats that are characterized by sparse emergent macrophyte cover and high light penetration to the water surface. Periphyton productivity is low in sawgrass stands in these same oligotrophic areas due to reduced light availability (Grimshaw et al., 1997; McCormick et al., 1998).

Consequently, sawgrass stands are characterized by low DO and a predominance of heterotrophic activity in the water-column compared with periphyton-dominated sloughs (Belanger et al., 1989; Rader, 1994).

Periphyton biomass and productivity peak towards the end of the wet season (August through October) and reach a minimum during the colder months of the dry season (January through March). Periphyton biomass in open-water habitats can exceed 1 kg/m^2 during the wet season (Wood & Maynard, 1974; Browder et al., 1982; McCormick et al., 1998), when floating mats can become so dense as to cover the entire water surface (Figure 3-6). Periphyton growth rates in open-water habitats are as much as 20-fold higher during the wet season compared with the dry season (Swift & Nicholas, 1987; McCormick et al., 1996). Seasonal fluctuations in periphyton gross primary productivity are similar but less dramatic, ranging between 3 to $8.5 \text{ g C/m}^2/\text{d}$ during the wet season compared with 1.6 to $6.7 \text{ g C/m}^2/\text{d}$ during the dry season (Browder et al., 1982; Belanger et al., 1989; McCormick et al., 1997; McCormick et al., 1998).



Figure 3-6. Typical distribution of periphyton (whitish floating material) within an oligotrophic slough in the northern Everglades (reference station U3, WCA-2A) during the summer wet season. Thick mats of periphyton typically are associated with the submerged macrophyte *Utricularia* and can completely cover the water surface in oligotrophic, open-water areas of the Everglades during the summer months and provide food and habitat for invertebrates and small fish. A benthic layer of periphyton (not shown in picture) is maintained in these habitats throughout the year. Sparse vegetation includes *Nymphaea* (floating leaves) and *Eleocharis* (erect stems).

The chemical composition of periphyton in the oligotrophic Everglades is indicative of severe P limitation. Periphyton samples from interior areas across the Everglades are characterized by an extremely low P content (generally <0.05%) and extremely high N:P ratios (generally >60:1 weight:weight) that are indicative of strong P limitation (Swift & Nicholas, 1987; Grimshaw et al., 1993; McCormick et al., 1998). This observational evidence for P limitation is supported by experimental fertilization studies that have shown that: (1) periphyton responds more strongly to P enrichment than to enrichment with other commonly limiting nutrients such as nitrogen (Scheidt et al., 1989; Vymazal et al., 1994); (2) periphyton changes in response to experimental P enrichment mimic those that occur along enrichment gradients in the marsh (McCormick & O'Dell, 1996). Thus, it is well established that periphyton is strongly P-limited in oligotrophic areas of the Everglades.

Oligotrophic areas of the Everglades contain a characteristic periphyton flora that is adapted to low P availability and the ionic content of the surface water in a particular area (Swift & Nicholas, 1987). Mineral-rich waters, such as those found in WCA-2A and Taylor Slough (the Park), support a periphyton assemblage dominated by a few species of calcium-precipitating cyanobacteria and diatoms. This assemblage appears to be favored by waters that are both low in P and at or near saturation with respect to calcium carbonate (CaCO₃) (Gleason & Spackman, 1974), the latter condition reflecting the influence of the limestone geology of the region. In contrast, interior waters of the Refuge contain an assemblage of desmids (green algae) and diatoms adapted to the extremely low mineral content of waters in this marsh. Waters across much of the southern Everglades (WCA-3A, Shark Slough) tend to be intermediate with respect to mineral content and contain taxa from both assemblages just described.

Vegetation

Located in the transition zone between temperate and tropical areas, the Everglades flora has many representatives from these two areas (39% and 61%, respectively) (Ewel, 1986; Gunderson, 1994), as well as taxa that are endemic to the region (Long, 1974). The vegetation communities characteristic of the pristine Everglades are dominated by species adapted to low P, seasonal patterns of wetting and drying, and periodic natural disturbances such as fire, drought, and occasional freezes (Duever et al., 1994; Davis, 1943; Steward & Ornes, 1975, 1983; Parker, 1974). Major wetland habitats that have been altered by P enrichment include sawgrass marshes, wet prairies, and sloughs (Loveless, 1959; Gunderson, 1994). The spatial arrangement of these habitats is constantly changing as a result of temporal and spatial variation in environmental factors such as fire, water depth, nutrient availability, and local topography (Loveless, 1959).

Sawgrass is the dominant macrophyte in the Everglades, and stands of this species comprise approximately 65 to 70% of the total vegetation cover of the Everglades (Loveless, 1959). Two types of sawgrass marshes have been identified in the Everglades interior: (1) dense stands of tall plants; and (2) sparse stands of short plants (Loveless, 1959; Wood & Tanner, 1990; Gunderson, 1994; Miao & Sklar, 1998). Tall, dense stands are generally monotypic, whereas sparse stands can be mixed with a variety of other sedges, grasses, herbs, and attached emergent or floating aquatic plants. The distribution of these two types of sawgrass marshes may be determined by the combined effects of soil type, nutrient availability, and fire frequency.

Wet prairies include a collection of low-stature, graminoid (grasslike) marshes occurring on both peat and marl soils (Gunderson, 1994). Wet prairies over peat occur in the wetter areas of the Everglades

and are composed of species such as beakrush (*Rhynchospora*), maidencane (*Panicum*), and spikerush (*Eleocharis*) (Loveless, 1959; Craighead, 1971). Wet prairies over marl are dominated by muhly grass (*Muhlenbergia filipes*) and sawgrass and occur in the southern Everglades on the east and west margins of the Shark River Slough and Taylor Slough, where bedrock elevations are slightly higher and hydroperiods shorter (Gunderson, 1994).

Sloughs are deeper water habitats that remain wet most or all of the year and are characterized by floating macrophytes such as fragrant white water lily (*Nymphaea odorata*), floating hearts (*Nymphoides aquaticum*), and spatterdock (*Nuphar luteum*) (Loveless, 1959; Gunderson, 1994). Submerged aquatic plants, primarily bladderworts (*Utricularia* spp.), also can be abundant in these habitats and provide a substrate for the formation of dense periphyton mats (described above).

Historically, cattail (*Typha* spp.) was just one of several minor macrophyte species native to the Everglades marsh (Davis, 1943; Loveless, 1959). In particular, cattail is believed to have been associated largely with areas of disturbance such as alligator holes and recent burns (Davis, 1994). Analyses of Everglades peat deposits reveal no evidence of cattail peat, although the presence of cattail pollen indicates its presence historically in some areas (Gleason & Stone, 1994; Davis et al., 1994; Bartow et al., 1996). Findings such as these confirm the historical presence of cattail in the predrainage Everglades, but provide no evidence for the existence of dense cattail stands covering large areas (Wood & Tanner, 1990; Bartow et al., 1996) as now occurs in the northern Everglades. In contrast, sawgrass and water lily peats have been a major freshwater component of Everglades soils for approximately 4,000 years (McDowell et al., 1969).

Fauna

Everglades fauna comprises a diversity of animals that depend on marsh primary production and ranges from microscopic invertebrates to top predators such as wading birds and alligators. While these organisms do not respond directly to increased P loading, they are affected by P-related changes in periphyton and vegetation and associated habitat modifications.

Invertebrates

Aquatic invertebrates (e.g., insects, snails, crayfish) represent a key intermediate position in the Everglades food web as these taxa (species) are the principal consumers of marsh primary production and, in turn, are consumed by vertebrate predators. The macroinvertebrate fauna of the Everglades is relatively diverse (approximately 200 taxa identified) and is dominated by Diptera (49 taxa), Coleoptera (48 taxa), Gastropoda (17 taxa) Odonata (14 taxa), and Oligochaeta (11 taxa) (Rader, 1999). Most studies have focused on a few conspicuous species (e.g., crayfish and apple snails) considered to be of special importance to vertebrate predators, and relatively little is known about the distribution and environmental tolerances of most taxa. An assemblage of benthic microinvertebrates (meiofauna) dominated by Copepoda and Cladocera also is present in the Everglades (Loftus et al., 1986), but even less is known about the distribution and ecology of these organisms.

Invertebrates occupy several functional niches within the Everglades food web; however, most taxa are direct consumers of periphyton and/or plant detritus. For example, almost 80% of the invertebrates collected from interior sloughs in WCA-2A were classified as consumers of either one or both of these food resources (Rader & Richardson, 1994). In contrast, relatively few taxa consume living macrophyte tissue. Rader (1994) sampled both periphyton and macrophyte habitats in this same area and, based on the

proportional abundance of different functional groups, suggested that grazer (periphyton) and detrital (plant) pathways contributed equally to energy flow in the pristine Everglades food web.

Invertebrates are not distributed evenly among Everglades habitats but, instead, tend to be concentrated in periphyton-rich habitats such as sloughs. In an early study, Reark (1961) noted that invertebrate densities in the Park were higher in periphyton habitats than in sawgrass stands. Rader (1994) reported similar findings in the northern Everglades and found mean annual invertebrate densities to be more than six-fold higher in sloughs than in sawgrass stands. Invertebrate assemblages in sloughs were more species-rich and contained considerably higher densities of most dominant invertebrate groups (**Figure 3-7**). Functionally, invertebrate assemblages in sloughs contained similar densities of periphyton grazers and detritivores, compared with a detritivore-dominated assemblage in sawgrass stands. Higher invertebrate densities in sloughs were attributed primarily to abundant growths of periphyton and submerged vegetation, which provide oxygen and a source of high-quality food. Within slough habitats, the greatest abundance of invertebrates occurs in benthic and floating periphyton (SFWMD, unpublished data), providing further evidence of the linkage between periphyton and invertebrates.

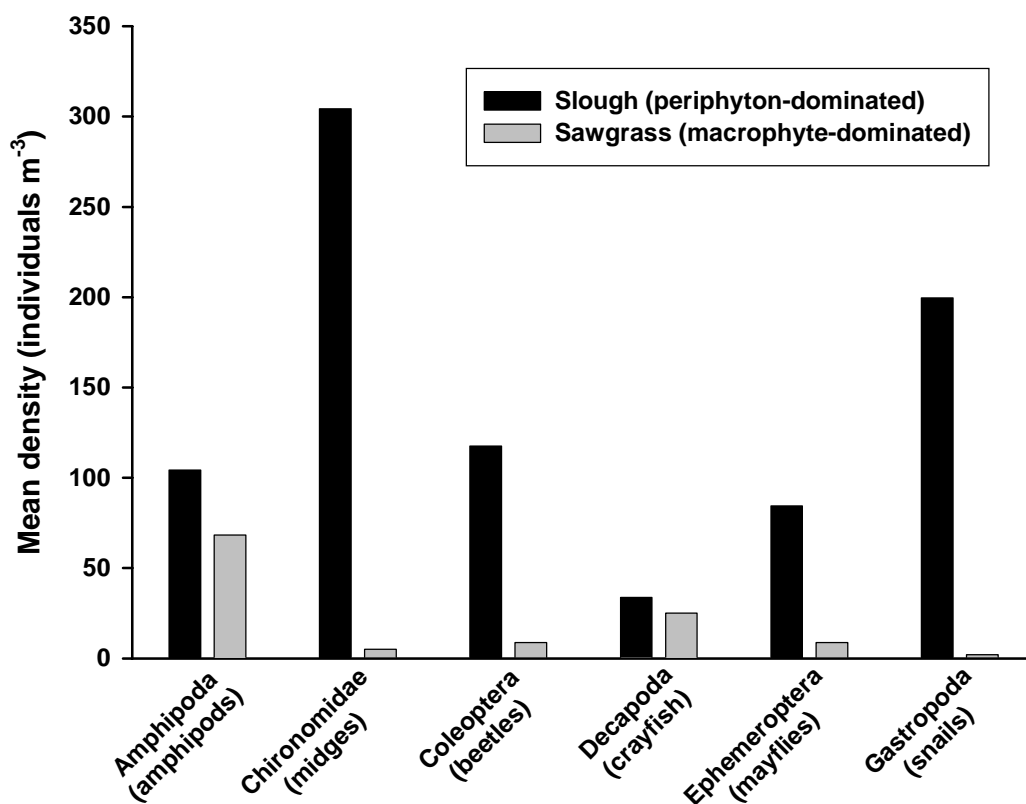


Figure 3-7. Densities of dominant groups of macroinvertebrates in periphyton-dominated (sloughs) and macrophyte-dominated (sawgrass stands) habitats in interior, oligotrophic areas of WCA-2A. Adapted from Rader (1994).

Higher trophic levels

The Everglades fish community in spikerush and sawgrass habitats contains about 30 species dominated by killifishes, livebearers and juvenile sunfishes (Loftus & Eklund, 1994). Species in deeper, open-water alligator holes include Florida gar, yellow bullhead, and adult sunfishes. A comparison of fish biomass between the Everglades and other freshwater marshes revealed that the Everglades has some of the lowest values (Turner et al., in press). Averaged across three to five seasons and nine sites, average fish biomass was 0.61 g/m² in the Everglades. Published mean values for other wetlands ranged from 1.4 to 513 g/m² (Turner et al., in press).

The breeding bird community in the central Everglades has fewer species than those in more northern wetlands (Brown & Dinsmore, 1986) or in Texas coastal marshes (Weller, 1994). The average number of species in the Everglades was 2.3 per site, and the number of individuals averaged 4.3 per site (Gawlik & Rocque, 1998). In contrast to the depauperate breeding bird community, the Everglades does support a large number of winter residents and may provide critical habitat for many species of trans-gulf migrants that winter in the tropics.

Wading birds are one group of birds that historically were very abundant in the Everglades as compared to other regions. Populations of some species are reported to have declined 90% since the 1930s (Ogden, 1994). Loss of habitat and changes in hydrology are two of the most often cited reasons for the declines. It is thought that even though the Everglades is an oligotrophic system it was able to support large numbers of top predators because of seasonal dry-downs in water levels, which concentrated fish and other aquatic prey items from large areas into small pools of receding water (Kushlan, 1986).

Patterns of P Enrichment in the Marsh

While atmospheric deposition remains the primary source of P for the Everglades, canal inputs have contributed additional P in the form of agricultural runoff to all areas of the Everglades in recent decades. These inputs have created zones of P enrichment within the marsh, with the most extensive enrichment occurring in the northern Everglades.

Marsh Water-Column P Concentrations

Canal discharges into the Everglades are elevated in P (and other elements, see **Chapter 4**) compared with interior areas of the marsh. Changes in water-column P concentrations have been documented downstream of these discharges in several parts of the Everglades. As described below, the degree and spatial extent of P enrichment varies among different areas of the marsh depending on the source and location of inflows, topography, and presence of interior canals.

WCA-2A

The largest database of marsh P exists for WCA-2A, where spatially intensive sampling has been conducted during the past two decades. Canal waters originating from the EAA enter this marsh through the S10 structures located along the northern levee (**Figure 3-8a**) and flow southward to create a P gradient that currently extends as far as 7 km into the marsh (McCormick et al., 1996; Smith & McCormick, in

review). Smaller volumes of EAA drainage water are discharged into the southwestern portion of this marsh through the S7 pump station and are associated with P enrichment in that area of the marsh.

Background water-column TP concentrations in WCA-2A are illustrated by data collected from five sampling stations in the marsh interior (**Figure 3-8b**). Mean TP concentrations near 10 $\mu\text{g/L}$ and median concentrations between 7 and 8 $\mu\text{g/L}$ are maintained throughout this area. The most complete data set for this marsh exists for station U3 and includes several samples with extremely high TP concentrations. Many of these high TP values likely resulted from sample contamination at low water depths, and therefore do not reflect typical water-column concentrations in the marsh interior

Water chemistry changes along the enrichment gradient south of the S10s (S10A-S10E) currently are being monitored with a network of 15 fixed sampling stations located 0 to 14 km downstream of canal discharges (**Figure 3-8a**). McCormick et al. (1996) summarized current patterns of P enrichment among these stations during 1994 and 1995 (**Figure 3-8c**). The mean TP concentration during this period was 104

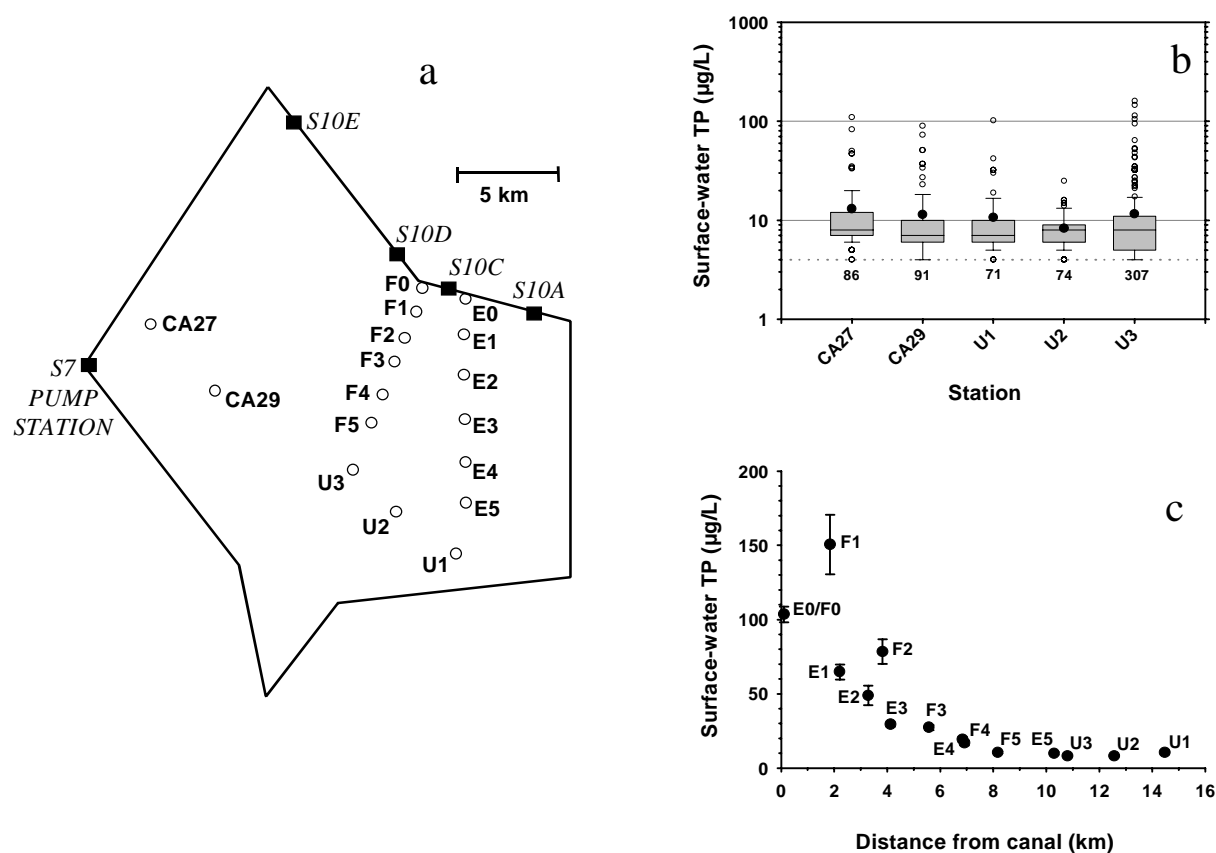


Figure 3-8. a. Permanent marsh and canal stations (E0 and F0) currently being sampled to document water chemistry in the marsh interior and along a nutrient-enrichment gradient in WCA-2A. Major inflow structures (closed squares) are italicized. b. Average water-column TP concentrations and ranges for sampling stations in the marsh interior (see **Figure 3-2** for interpretation of box plots). c. Mean (± 1 SE) water-column TP concentrations at stations downstream of the S10s between 1994 and 1997 (from McCormick et al., 1996).

$\mu\text{g/L}$ immediately downstream of canal discharges compared with mean concentrations of $< 11 \mu\text{g/L}$ at interior stations $> 8 \text{ km}$ downstream. Declines in SRP, an indicator of bioavailable P, were of a similar magnitude, and averaged $48 \mu\text{g/L}$ just downstream of the canal compared with $< 4 \mu\text{g/L}$ (detection limit) at interior marsh stations. These declines in water-column P concentrations are substantially higher than could be explained by dilution alone, and reflect biological and chemical removal of this limiting nutrient by the soils and marsh biota as discussed elsewhere in this chapter.

Long-term changes in water-column TP in this marsh between 1978 and 1997 were assessed using data from 49 marsh stations (including those described above) that had been sampled for varying periods of time during the past two decades (Smith & McCormick, in review). Total P concentrations, both in canal discharges and the marsh, generally increased through the mid-1980s and then decreased into the early 1990s. These patterns are consistent with trends detected for canal discharges across the Everglades (Walker, in press), suggesting a linkage to changes at the watershed scale (e.g., implementation of BMPs, weather patterns). In the marsh, this trend was correlated inversely with marsh stage and rainfall, both of which were low during drought years in the mid and late 1980s, and relatively high in the late 1970s and 1990s. Thus, changes in the P gradient are influenced by interannual changes in marsh hydrology as well as canal P concentrations and loads. Results of this analysis also indicated that temporal changes in the marsh varied as a function of distance from the canal. Specifically, movement of a water-column P front into the marsh during the 1980s (generally low water years) and a recession during the early 1990s (higher water years) were evident at sampling stations closer to the canal, whereas stations further into the marsh showed little if any decline during the 1990s and did not approach 1970s concentrations (**Figure 3-9**).

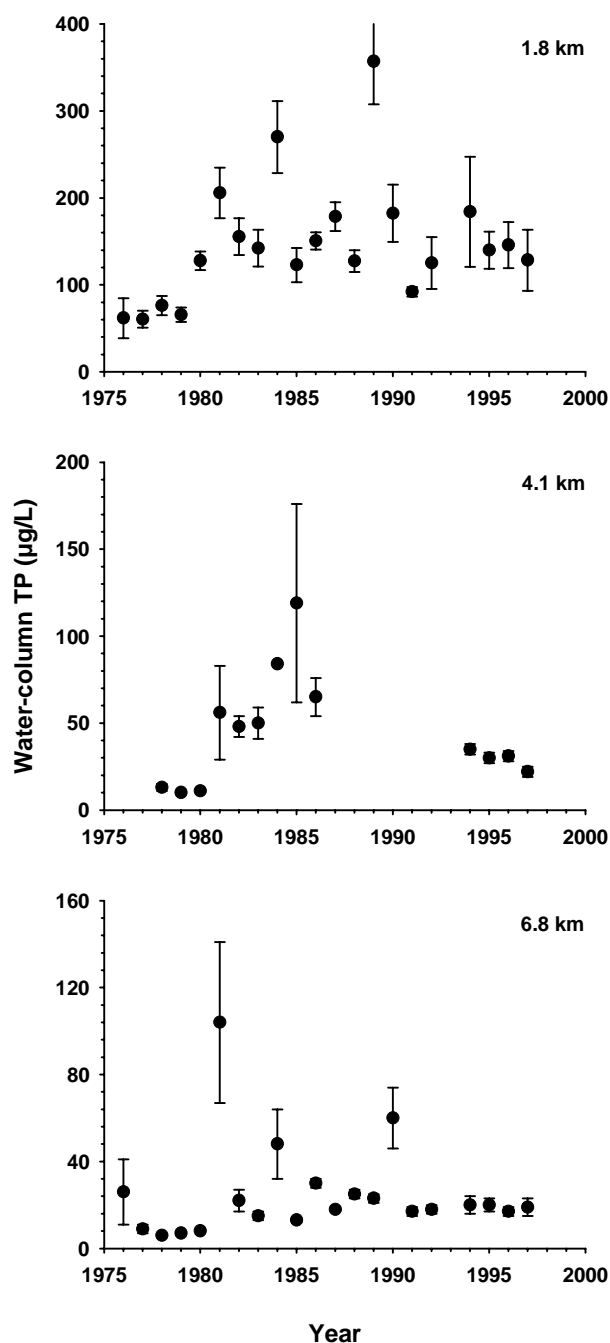


Figure 3-9. Interannual variation in water-column TP concentrations (mean \pm 1SE) at three long-term sampling stations located 1.8, 4.1, and 6.8 km downstream of the S10s. Based on the data set compiled and analyzed by Smith & McCormick (in review).

The Loxahatchee National Wildlife Refuge

The Refuge is exposed to the same EAA drainage that has caused extensive P enrichment in WCA-2A. However, whereas these discharges enter WCA-2A as sheet flow, intrusions of P-enriched waters into the Refuge generally are restricted to the marsh perimeter. Data collected from a network of 14 sampling stations in this marsh illustrate this pattern (**Figure 3-10a**). These stations, all of which are located >1 km into the marsh, generally maintain water-column TP concentrations < 10 µg/L (**Figure 3-10b**).

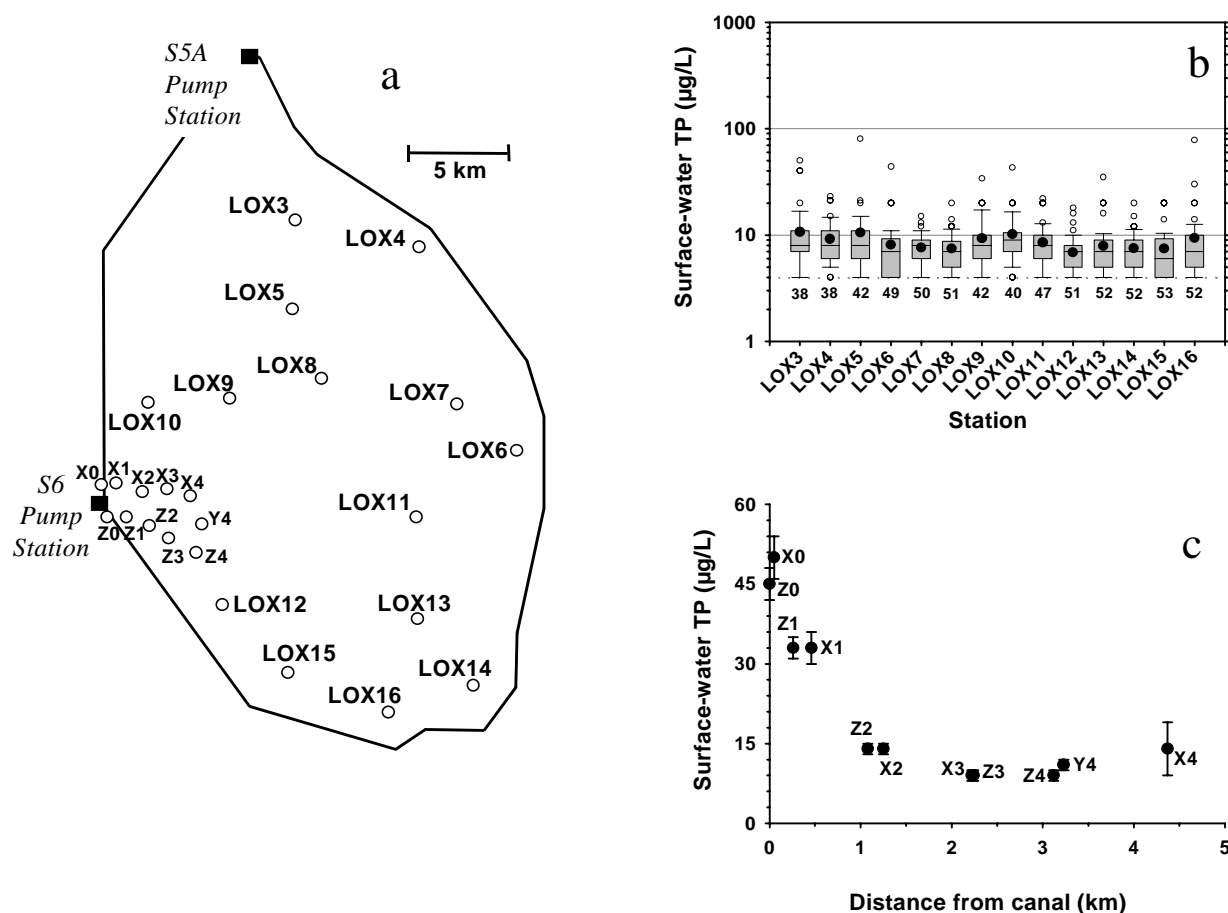


Figure 3-10. **a.** Permanent marsh and canal (X0 and Z0) stations currently being sampled to document water chemistry changes in the marsh interior and along a nutrient-enrichment gradient in the Refuge. Major inflow structures (closed squares) are italicized. **b.** Average water-column TP concentrations and ranges for sampling stations in the marsh interior sampled since 1993 (see **Figure 3-2** for interpretation of box plots). **c.** Mean (\pm 1SE) water-column TP concentrations at stations in proximity to the S6 pump station during the period between April, 1996 and October, 1997.

To document changes within perimeter areas, the District began collecting water samples monthly beginning in April 1996 at nine marsh stations and two canal stations in the southwest corner of the Refuge (**Figure 3-10a**). Water quality changes in this area reflect the combined effects of S5A and S6 discharges. As documented in WCA-2A, water-column P concentrations decrease exponentially with increasing distance from the canal (**Figure 3-10c**). However, the water quality gradient in the Refuge is rather steep, indicating that canal waters seldom intrude as far into this marsh as in WCA-2A. Mean TP concentrations between April 1996 and October 1997 were 44 and 51 $\mu\text{g/L}$ at the two canal stations, compared with concentrations around 10 $\mu\text{g/L}$ at marsh sites > 2 km from the canal. Higher mean TP at the most interior site (Z4) during 1997 was the result of a single extreme measurement (130 $\mu\text{g/L}$) recorded on March 25, 1997. Mean SRP ranged between 15 and 19 $\mu\text{g/L}$ in canal waters, and decreased to between 3 and 4 $\mu\text{g/L}$ in the marsh interior.

WCA-3A

This area is bisected by the Miami Canal, which serves as a conduit for canal waters discharged through the S8 pump station (**Figure 3-11a**). The presence of this canal has caused northern portions of this marsh to become severely overdrained but has reduced the flow of P-enriched canal waters into these same areas. Enrichment in northern WCA-3A is greatest in areas adjacent to the Miami Canal, particularly near the S339 and S340 structures, where water is detained and spills over into the marsh. Similarly, urban and agricultural drainage into southeastern WCA-3A through S9 tend to be diverted away from the marsh by interior canals. Other areas subjected to enriched drainage water include the S11 and S150 structures in the north, which discharge from WCA-2A and the EAA, respectively, and the L28 intercept canal, which drains agricultural lands to the west.

Relatively few data are available to characterize P gradients in WCA-3A. Surface waters in the marsh interior are generally low in P as illustrated for District sampling stations that are distant from inflows (**Figure 3-11b**). Sampling in proximity to selected District structures (S9 and S339) in 1997 indicate modest water-column TP gradients extending as far as 3 km into the marsh (**Figures 3-11c**). However, the full extent of P enrichment within WCA-3A has not been characterized as thoroughly as for areas further north.

Everglades National Park

Water enters the Park in three principal locations (**Figure 3-12a**): (1) Shark Slough through the S12 and S333 structures located along Tamiami Trail; (2) Taylor Slough through S332; and (3) the C-111 canal in the east. The sources of these inflows include WCA-3A (S12s) and a network of canals draining agricultural and urban lands in the east (S332, C111). Phosphorus concentrations in these inflows are considerably lower than those entering the northern Everglades but still tend to be elevated compared with sampling stations in the interior of the Park, which exhibit some of the lowest water-column TP concentrations in the Everglades (**Figure 3-12b**). Phosphorus loads and flow-weighted TP concentrations in waters entering Shark Slough are five-fold and nearly two-fold higher, respectively, than those released into Taylor Slough and the C111 basin (Rudnick et al., in press). As for the northern Everglades, TP concentrations generally peaked during the drought years of the mid 1980s and have declined during the 1990s (Walker, in press).

The network of marsh sampling stations in the Park is less extensive than in northern areas of the Everglades, and consequently patterns of enrichment are more difficult to define. Data collected

downstream of the S12 structures during 1996 and 1997 show no discernible gradient in water-column TP (Figure 3-12c). However, elevated soil TP concentrations downstream of these inflows indicate that P enrichment has occurred in this area over the past several years (Raschke, 1993). Temporal and spatial changes in water-column P concentrations in different parts of the Park are discussed in greater detail by Walker (1997) and Rudnick et al. (in press).

Marsh Soil and Porewater P Concentrations

Since the early 1990s, an extensive soil coring effort has produced soil nutrient maps for various regions in the Everglades. These maps show that TP concentrations in soils near canals or other management structures are more than two-fold higher than concentrations in interior areas (Figure 3-13) Koch & Reddy, 1992; DeBusk et al., 1994; Reddy et al., 1994a; Reddy et al., 1994b; Newman et al., 1997). In the Refuge and WCA-2A, elevated TP concentrations are associated primarily with increased P loading from canal waters and have been linked directly to the use of fertilizer (Zielinski et al., 1997). By contrast,

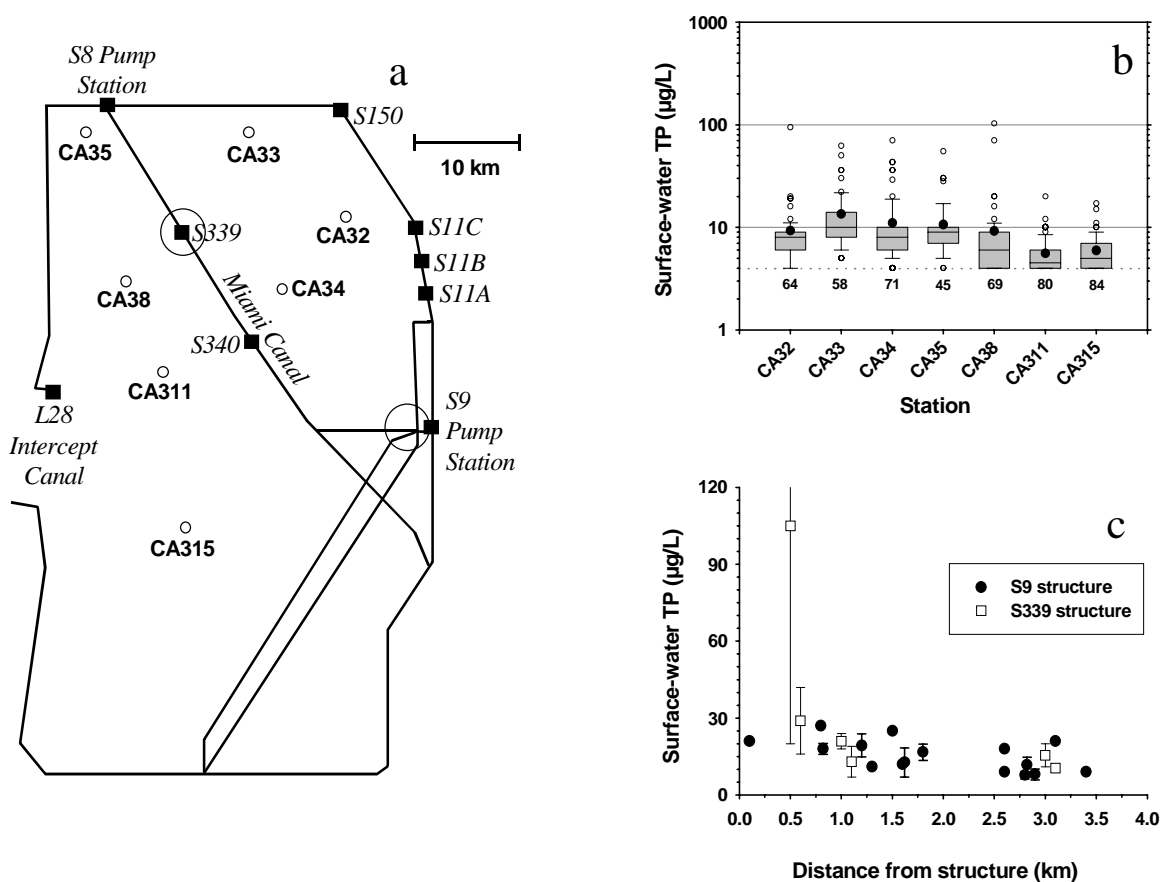


Figure 3-11. **a.** Permanent marsh stations currently being sampled to document water chemistry changes in the marsh interior in WCA-3A. Major structures (closed squares) are italicized. **b.** Average water-column TP concentrations and ranges for sampling stations in the marsh interior sampled since 1994 (see Figure 3-2 for interpretation of box plots). **c.** Mean (\pm 1SE) water-column TP concentrations at stations in proximity to the S9 and S339 structures (circled areas in Figure 3-11a) on two sampling events during the fall of 1997.

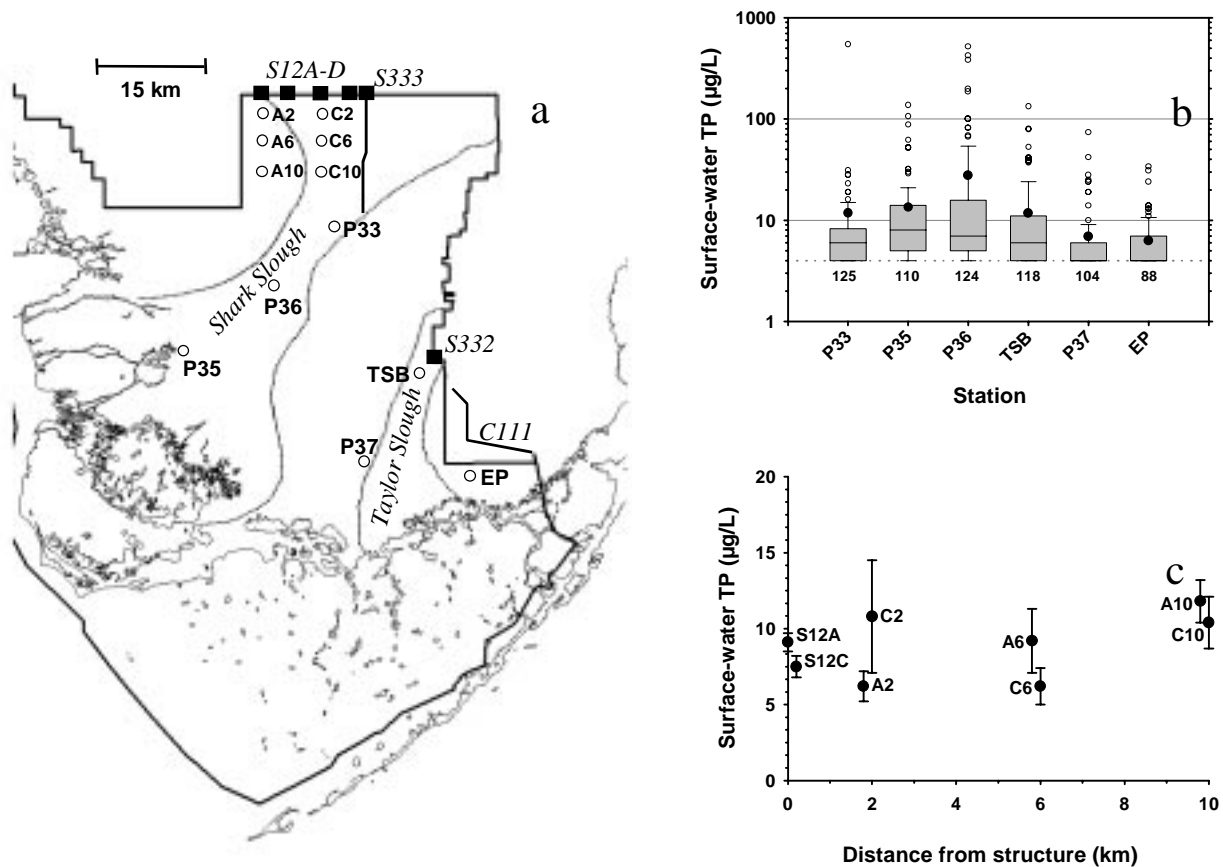


Figure 3-12. **a.** Permanent marsh stations currently being sampled to document water chemistry changes in the marsh interior of freshwater areas of the Park. Major inflow structures (closed squares) are italicized. **b.** Average water-column TP concentrations and ranges for sampling stations in the marsh interior (see **Figure 3-2** for interpretation of box plots). **c.** Mean (\pm 1SE) water-column TP concentrations at stations downstream of the S12 structures during 1997.

increased soil TP in Holey Land, Rotenberger and northern WCA-3A largely appear to be a function of overdrainage of these soils, with resultant soil compaction and nutrient concentration as illustrated by increased soil bulk densities and elevated nutrients (Newman et al., 1998).

Analysis of spatial soils data from the Refuge, WCAs, and Holey Land suggests that the influence of P loading on Everglades soils generally is restricted to a distance of approximately (\sim) 5 km from inflow structures or canals (Reddy et al., 1998). In most cases, these spatial soils data represent a single point in time. However, an intensive study of WCA-2A has resulted in the establishment of temporal as well as spatial responses to external P loads. Total P concentrations in surficial soils in WCA-2A have increased over three-fold since the 1970s. Soil cores encompassing the surface 0 to 10 cm soil depths were collected at sites 1.6, 3.2, and 6.4 km south of the Hillsboro Canal in 1975 and 1976 (Davis, 1989). Total P

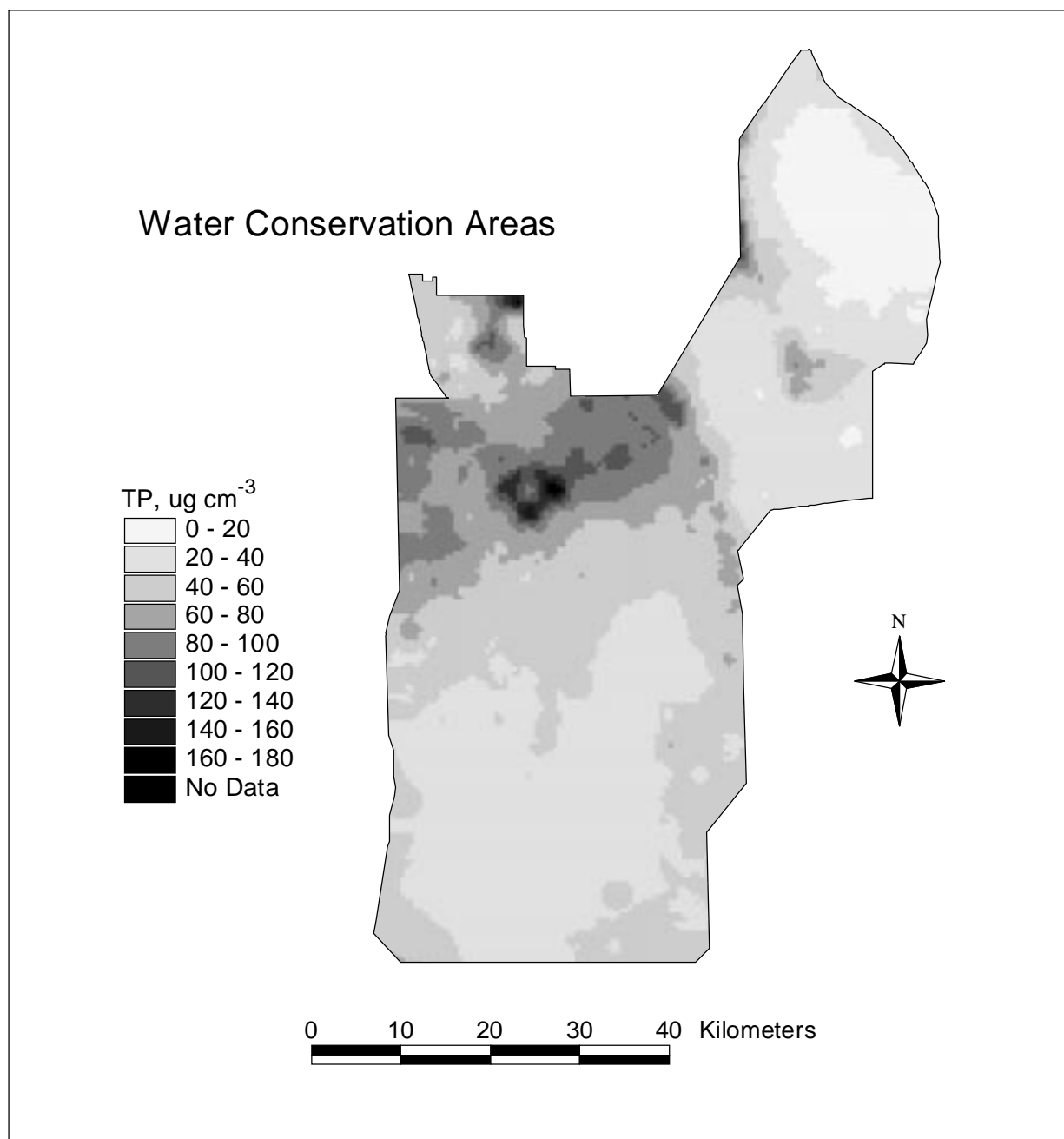


Figure 3-13. Distribution of TP content in the surface soils throughout the WCAs and Holey Land.

concentrations in soils within 1.6 km ranged 420 to 440 mg/kg, while cores at distances 3.2 and 6.4 km from inflow ranged between 310 and 340 mg/kg (Davis, 1989). Soils collected at the same depth from similar locations in 1990 showed that TP concentrations were > 1,500 mg/kg at a distance of 1.4, 1,100 mg/kg at 3.5 km, and only decreased to values consistently < 400 mg/kg at sites more than 9 km from the canal (Reddy et al., 1991; Koch & Reddy, 1992). These soils samples were not collected in identical locations nor analyzed using identical methods; therefore, differences in accuracy or precision certainly may exist. However, based on the magnitude of the change, it is still apparent that both soil TP concentrations in WCA-2A and the area influenced by external P loads has increased in recent decades. Recent soil coring indicates continuing enrichment between 1990 and 1996 in soils 2 to 7 km from the canal, compared with no increase in soils > 7 km from these inflow (**Figure 3-**) (Reddy et al., in press).

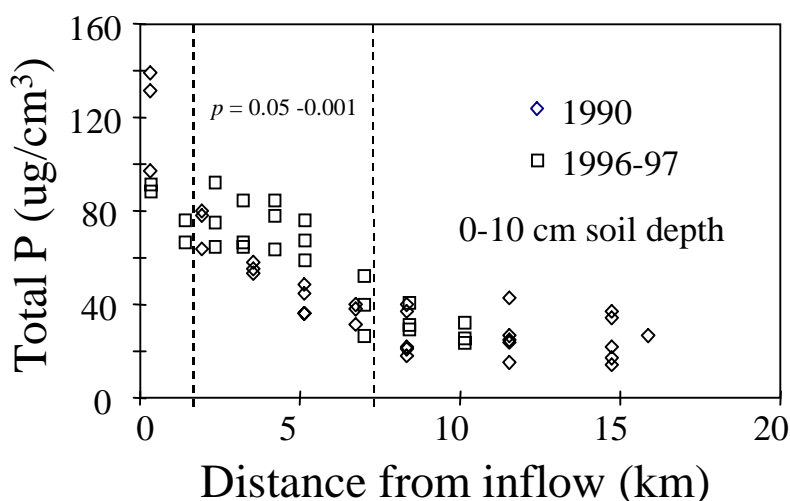


Figure 3-14. Total phosphorus content of soils (0-10 cm depth) downstream of the S10s in WCA-2A. Samples were collected July 1990; February and August, 1996; and March, 1997. Dashed lines show the distance range where significant ($0.050 < p < 0.001$) increases in soil TP were detected. From Reddy et al., 1998.

Other studies comparing soils along the same gradient suggest that no change in soil TP concentrations occurred during the 1990s (Richardson et al., 1997; Tetra Tech, 1998). The conclusions drawn by Tetra Tech (1998) are based on the collection of soil cores in 1997 within the same spatial grid of 74 sites originally sampled by Reddy et al. (1991) in 1990. Average soil TP concentrations downstream of the S10 inflow structures did not change significantly over the 7-year period. However, significant increases in soil P at sites furthest downstream where TP concentrations were < 500 mg/kg suggested that P enrichment had spread further into the marsh. Differences between specific conclusions drawn by Reddy et al. (1998)

and those of Richardson et al. (1997) and Tetra Tech (1998) may be attributed to different sampling techniques and the number of replicate samples collected. The coefficient of variation in soil TP concentrations (0-10 cm depth) measured on triplicate samples from sites in WCA-2A ranged from 6 to 48 (Reddy et al., 1991; Tetra Tech, 1998). Thus, the absence of replication will weaken the ability to detect statistically significant differences. Reddy et al. (1998) collected replicate cores during each sampling event and composited the 0-10 cm soil depth increment. In contrast, there was no apparent replication of cores by Richardson et al. (1997), and cores were sectioned into 2-cm intervals. Thus, the 0-10 cm soil TP concentration was a calculated average. In addition, the TP average should be weighted to account for bulk density of the different soil increments, and it is not clear if this was considered in the calculations of Richardson et al. (1997).

In general, the effect of P loading is restricted to the surface 30 cm of soil depth (Reddy et al., 1998). Vertical gradients of TP within the soils revealed that TP was highest in the surface soils and decreased with soil depth, with the steepest vertical gradient at sites closest to canal inflows (Koch & Reddy, 1992; Reddy et al., 1998). Concomitant with increased soil TP concentrations throughout the vertical profile, external P loading resulted in increased soil accumulation in areas of P enrichment. The vertical accretion of peat has been estimated by measuring the location of the ^{137}Cs peak within a soil depth profile. The ^{137}Cs peak corresponds to the soil surface in 1964; the average post-1964 accumulation is then calculated as the depth of soils to the peak divided by the difference between the soil collection date and 1964. Peat accretion rates in WCA-2A reached a maximum of 1.1 cm/yr at a distance of 0.3 km from inflow, and decreased logarithmically with distance to less than 0.25 cm/yr in interior areas of the marsh (Craft & Richardson, 1993a; Craft & Richardson, 1993b; Reddy et al., 1993). These peat accretion rates produced corresponding P accumulation rates of 0.46 to 1.1 g/m²/yr in cattail dominated, i.e., enriched soils, and 0.06 to 0.25 g/m²/yr in unenriched soils. In the Refuge, soil accumulation rates range from 0.07 to 0.42 cm/yr in unenriched and enriched soils, while much lower accumulation rates were observed in the northern end of WCA-3A (0.04 to 0.28 cm/yr) (Craft & Richardson, 1993a; Robbins et al., 1996).

The influence of external P loads on Everglades soil chemistry is a slow process. The component that is first and most impacted by elevated P loads is the flocculent layer of material resting on the soil surface, which is comprised of unconsolidated plant detritus and/or benthic periphyton. A field P loading experiment conducted in WCA-2A showed elevated P concentrations in the benthic periphyton within one month of the start of P addition (Newman et al., in preparation). In contrast, increased P concentrations in the surficial (0 to 3 cm) soil layer were observed after one year, and only at the highest loading rate of 12.8 g P/m²/yr. Similar results were obtained by Richardson & Vaithyanathan (1995) who found that TP concentrations in the surficial sediment-periphyton layer increased two-fold in P-enriched flume channels compared with unenriched controls after two years of dosing, whereas no increase in soil TP was observed. Following the disappearance of the benthic periphyton in response to P loading, it is anticipated that external P loads will penetrate further into the soil profile.

The ability of Everglades soils to act as a sink or source for P is dependent on the forms of P that accumulate. The Everglades are underlain by carbonate-rich sediments and are exposed to calcium (Ca)-rich surface water. Therefore, soil P chemistry likely is influenced by interactions with Ca and magnesium (Mg) carbonates, resulting in the production of both unstable and stable forms of Ca and Mg phosphates. The most conventional approach to the identification of P in soils is through extraction with different chemicals (Newman & Robinson, in press). Using fractionation procedures, it has been shown that P is stored primarily as organic P, with approximately one-third of TP stored as inorganic P (primarily Ca- and Mg-bound P) (Qualls & Richardson, 1995; Reddy et al., 1998). Phosphorus chemistry in wetlands also may be controlled by other nutrients, such as iron (Fe). Unlike Ca phosphate, Fe phosphate chemistry is influenced by the redox condition of the soil, i.e., whether the soils are aerobic or anaerobic. Under anaerobic conditions, Fe phosphates are soluble and P is more readily available. It is unlikely that Fe dominates P cycling in the Everglades because soil Fe concentrations are extremely low (<1%) and the soils are high in organic matter and sulfur, both of which interact with Fe to influence its solubility and bioavailability.

As discussed previously, peat accreted faster in P-enriched areas; therefore, different P forms also accumulated faster in enriched areas. A comparison of the accumulation of different P forms along the nutrient gradient in WCA-2A revealed that organic P compounds accumulated at rates seven to 8.2 times

faster in enriched than unenriched areas, Ca-bound P accumulated 6.7 times faster, and microbial biomass and Fe/Al bound inorganic P accumulated between two and three times faster (Qualls & Richardson, 1995).

Fractionation procedures also identify forms as labile, i.e., those that are easily transformed or exchanged, or resistant. The labile forms will have a significant influence on the P concentration in porewater that is in equilibrium with the soils. As a result, porewater P concentrations follow the same trends as those observed in soils, showing an exponential decrease in concentrations with increasing distance from canal discharges. Unlike soils, however, porewater P concentrations tend to have high seasonal variability at enriched sites, but not unenriched sites (Koch-Rose et al., 1994). Enriched areas of the Refuge and WCA-2A have SRP concentrations $>1,000 \mu\text{g/L}$ in the surface 0 to 10 cm fraction (Koch & Reddy, 1992; DeBusk et al., 1994; Koch-Rose et al., 1994; Newman et al., 1997).

Ecological Responses to P Enrichment

Soil Microbes and Biogeochemical Processes

Increased nutrient loading to the Everglades has resulted in a gradient in the quality and quantity of organic matter, rates of nutrient accumulation, microbial biomass and community composition, and biogeochemical cycling downstream of canal discharges. This gradient has been documented in WCA-2A, the Refuge, Holey Land, and WCA-3A (Reddy et al., 1998). In oligotrophic interior areas of the Everglades, P is the primary factor limiting the microbial processes that control decomposition and nutrient cycling rates. Compared with the marsh interior, nutrient-enriched areas are characterized by the rapid turnover of organic matter, and by open elemental cycling, where nutrient inputs often exceed demand. These changes have important environmental and ecological consequences including: (1) a conversion from a P-limited to an N-limited system because of high P availability and increased biological demand for N; and (2) an accumulation of low N:P ratio detritus and accelerated rates of decomposition and nutrient cycling. Many biogeochemical processes that affect plant productivity and water chemistry are accelerated by P enrichment, resulting in the release of other plant nutrients such as N. The accumulation of P and other nutrients in the soils and biota, coupled with accelerated cycling rates may maintain eutrophic conditions in already enriched areas for some time following P load reductions.

All forms of P in the litter and surface (0-10 cm) soil layers increased with increasing P enrichment in WCA-2A (Reddy et al., 1998). Both the C:P ratio and potentially mineralizable organic P (PMP) of litter and soils at enriched sites were elevated compared with reference areas in the marsh. This increase in P availability and detritus quality was associated with an increase in microbial biomass and total activity. For example, in the litter layer of WCA-2A soils, microbial biomass C was approximately six-fold higher in enriched areas compared with unenriched locations. Microbial biomass C was higher in recently accreted detrital layers than the 0-10 cm soil layer (DeBusk & Reddy, 1998). Microbial respiration reflects the activity of microorganisms in detrital and soil layers. Addition of P to unenriched Everglades soil (230 mg P/kg) stimulated microbial respiration, measured as organic C mineralization, and resulted in a shift towards anaerobic respiration (Bachoon & Jones, 1992; Amador & Jones, 1993). Correspondingly, enriched soils contained between 10^3 - and 10^4 -fold higher numbers of anaerobes, including methanogens, sulfate reducers, and acetate producers, than unenriched soils in the marsh interior (Drake et al., 1996).

Addition of electron acceptors (such as O_2 , NO_3^- , and SO_4^{2-}) accelerated microbial respiration in WCA-2A soils, indicating that microbial activity is limited by the availability of suitable electron acceptors as well as P (Wright & Reddy, in preparation). Consumption of these electron acceptors during microbial respiration was higher in soils collected from P-enriched area of WCA-2A than in reference areas (Fisher 1997), providing further evidence of the stimulation of various microbial pathways by canal inflows.

Microbes produce a wide range of extracellular enzymes that catalyze the decomposition of organic matter (Sinsabaugh, 1994). Among the enzymes measured in detrital and soil layers in WCA-2A, alkaline phosphatase activity (APA), an indicator of P mineralization, decreased with P enrichment, while B-D glucosidase, a measure of C mineralization, increased (Wright & Reddy, 1996). Arylsulfatase and phenol oxidase activity was unrelated to P loading. Enzyme activity was highest in the detrital layer and decreased with increasing soil depth. Phosphatase activity showed the strongest relationship with canal inputs, indicating the controlling influence of P loading on microbial processes (Wright & Reddy, 1996). The use of APA as an indicator of P enrichment is discussed further under periphyton responses (see below).

Increased P loading to the northern Everglades is associated with dramatic changes in the cycling of other biologically important elements such as N. Organic N mineralization occurs through: (1) hydrolytic deamination of amino acids and peptides; (2) degradation of nucleotides; and (3) metabolism of methylamines by methanogenic bacteria (King et al., 1983). Potentially mineralizable N (PMN) was estimated to be 3.5-fold and 1.7-fold higher, respectively, for litter and 0-10 cm layers of P-enriched soils in WCA-2A than in unenriched soils (White & Reddy, 1997). Higher rates of N mineralization were suggested in enriched areas and were attributed to low detritus C:N ratios and P-non-limiting conditions (Koch-Rose et al., 1994). Under P-enriched conditions, it is likely that the growth of cattail is enhanced by this increased availability of N.

Nitrification, the biological conversion of reduced N forms (NH_4-N) to more oxidized states (NO_3-N), is a key process in the N budget of wetland systems, since the NO_3 formed is available for macrophyte and periphyton growth. More importantly, nitrification provides the substrate (NO_3) for denitrification, a second biological process whereby NO_3 (or NO_2) is converted into gaseous endproducts such as N_2O and N_2 that are lost to the atmosphere. Nitrification rates appear to be limited by P in oligotrophic areas and are elevated both in detrital and surface soil layers in P-enriched locations (Reddy et al., in press). Denitrification rates, as indicated by the activity of denitrifying enzymes, also are higher in enriched areas near canal inflows (White & Reddy, 1997). However, this response more likely is related to high NO_3^- loads at these inflow points than to P enrichment.

Phosphorus loading to wetlands increases the P concentration of periphyton mats and can result in a shift towards N limitation (see periphyton responses below). Such conditions promote the growth of nitrogen-fixing species that are capable of converting inert N_2 gas into bioavailable N (NH_3). Biological fixation in periphyton mats obtained from enriched locations were higher than those from a reference area of WCA-2A (P. Inglett, unpublished data).

Periphyton

Periphyton is sensitive to changes in water-column P concentrations and rapidly accumulates P from the water as it becomes available (Davis, 1982; McCormick et al., 1998). Thus, a strong relationship between water-column and periphyton P concentrations is maintained along marsh P gradients downstream of canal inflows (**Figure 3-15a**) (Grimshaw et al., 1993; McCormick & O'Dell, 1996). Field dosing experiments also have shown that periphyton accumulates P in proportion to the loading rate, and that this accumulation can be detected within weeks at loading rates similar to those in highly enriched areas of the Everglades. Periphyton P increased rapidly and by as much as 10-fold within field enclosures receiving weekly pulses of SRP (loading rate = 0.25 g/m²/wk), while no changes in soil or macrophyte P content were detected even after several months of dosing (**Figure 3-15b**) (McCormick & Scinto, in press). These findings are consistent with earlier work by Davis (1982), who found that periphyton mats concentrated radio-labelled SRP at a faster rate than either macrophytes or soils on a biomass-specific basis.

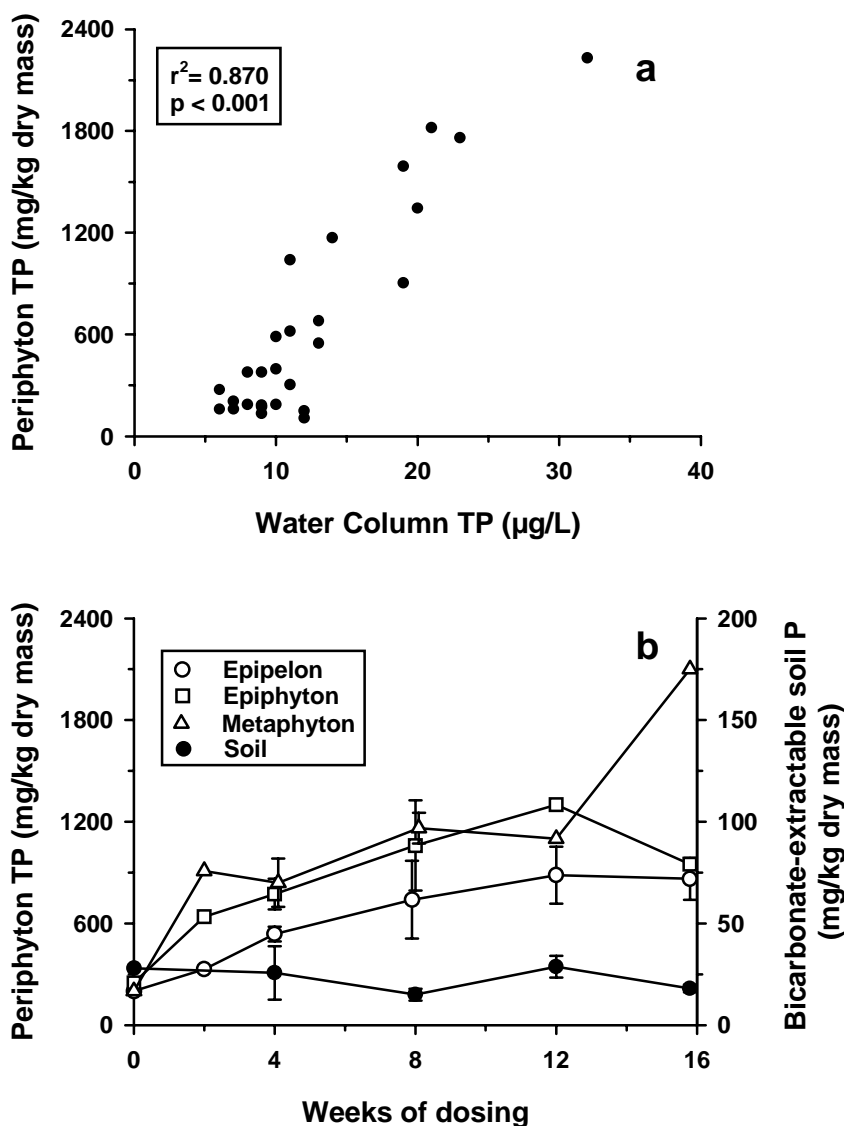


Figure 3-15. **a.** Relationship (Pearson's product-moment correlation coefficient) between water-column TP concentrations and the P content of floating periphyton mats collected downstream of the S10s in WCA-2A. **b.** Accumulation of P in periphyton components and soils in response to weekly P additions to experimental plots in an oligotrophic slough in the interior of WCA-2A. From McCormick & Scinto (in press).

Physiological changes in the periphyton mat occur rapidly as internal P concentrations increase. Two physiological responses to P enrichment that have been well documented in the Everglades are a decrease in phosphatase activity (PA) and an increase in cell metabolism (McCormick & Scinto, in press;

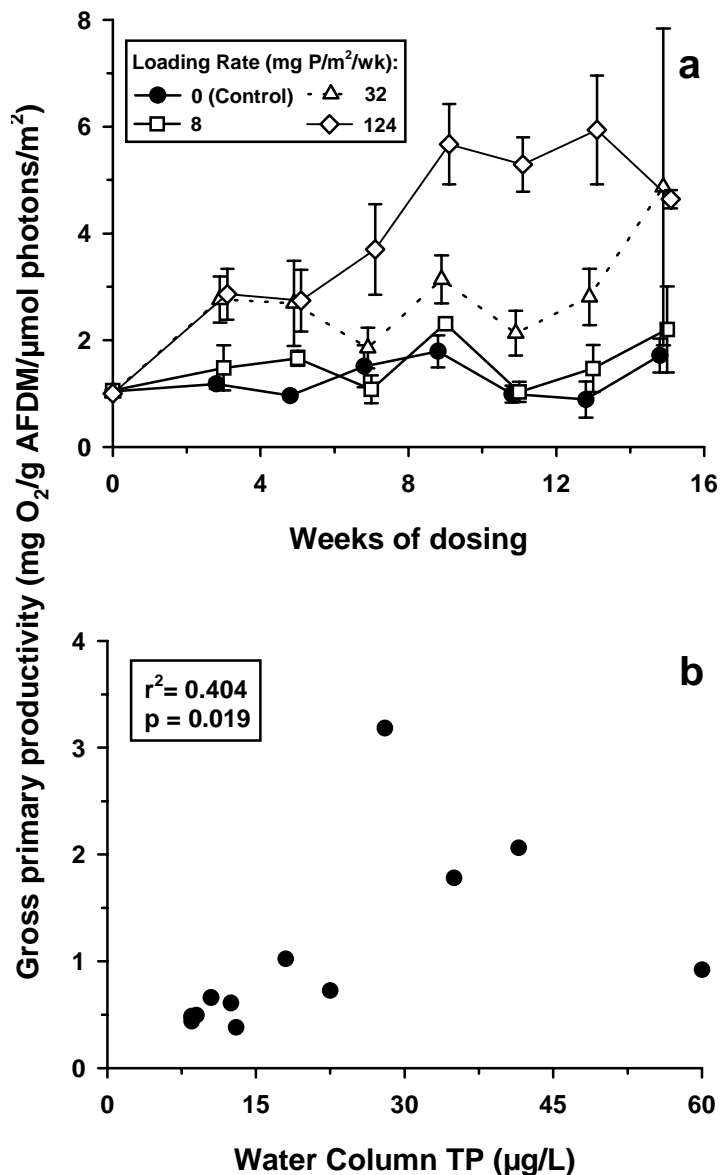


Figure 3-16. **a.** Changes in the productivity of floating periphyton mats in experimental slough plots in WCA-2A exposed to different loading rates of P (McCormick & Scinto, in press). **b.** The relationship between floating mat productivity and water-column TP downstream of the S10s in WCA-2A (McCormick, unpubl. data).

Newman et al., in press). Phosphatases are enzymes that allow microbes to scavenge P from the surrounding environment. Algal and bacterial production of these enzymes decreases as internal stores of P increase in response to P enrichment. Such decreases have been documented along P gradients in the Everglades (USEPA, 1998) and in field P-dosing experiments (Newman et al., in press), indicating that the limiting influence of P on periphyton metabolism and growth is reduced near canal inflows.

Relaxation of P limitation stimulates periphyton photosynthesis and respiration, the processes that allow for the fixation and utilization of energy for growth. The primary productivity of periphyton mats in the oligotrophic interior of WCA-2A increased by as much as three-fold within three weeks in response to weekly P additions to field mesocosms (**Figure 3-16**) (McCormick & Scinto, in press). Similar changes have been documented along P gradients in this same marsh (**Figure 3-16**). Similarly, periphyton growth rates on artificial substrata are correlated strongly with increases in water-column TP and can be more than 10-fold higher in highly enriched areas of the marsh compared with the oligotrophic interior (Swift & Nicholas, 1987; McCormick et al., 1996).

Elevated P loads and concentrations result in the loss of species adapted to survival under P-limited conditions and their replacement by species capable of higher growth rates under P-enriched conditions. One of the most pronounced changes involves the loss of the calcareous assemblage of cyanobacteria and diatoms, which is seasonally abundant in oligotrophic, mineral-rich

waters that cover large areas of the Everglades. This oligotrophic assemblage is replaced by a eutrophic assemblage of filamentous cyanobacteria, filamentous green algae, and diatoms in enriched areas of the marsh (Swift & Nicholas, 1987; McCormick & O'Dell, 1996). Some of these potential indicator taxa are listed in **Table 3-1**. Surveys of periphyton and water quality throughout the Everglades (Swift & Nicholas, 1987; Raschke, 1993; McCormick et al., 1996; Pan et al., 1997) have found consistently strong correlations between water-column P concentration and the abundance of several diatom species. Many of these species are recognized as reliable indicators of eutrophication in other freshwater ecosystems (e.g., Palmer, 1969; Lowe, 1974; Lange-Bertalot, 1979) and can be used to identify areas of the marsh affected by P-enrichment.

Controlled dosing studies have provided experimental evidence that species changes documented downstream of canal inflows result primarily from P enrichment. In an early study in the Park, Flora et al. (1988) found that the calcareous periphyton assemblage indicative of oligotrophic conditions was lost from experimental dosing channels in response to P concentrations of < 20 µg/L SRP. McCormick & O'Dell (1996) compared taxonomic changes downstream of canal inflows into WCA-2A to those produced by P

Table 3-1. A list of some of the periphyton taxa that may indicate low P and high P availability in the Everglades as synthesized by McCormick and Stevenson (1998).

Group	Low P availability	High P availability
Cyanobacteria (blue-green algae)	<i>Oscillatoria limnetica</i> <i>Schizothrix calcicola</i> <i>Scytonema hofmannii</i>	<i>Oscillatoria princeps</i>
Bacillariophyta (diatoms)	<i>Amphora lineolata</i> <i>Anomoeoneis serians</i> <i>Anomoeoneis vitrea</i> <i>Cymbella lunata</i> <i>Cymbella turgida</i> <i>Synedra synegrotesca</i>	<i>Amphora veneta</i> <i>Epithemia adnata</i> <i>Gomphonema parvulum</i> <i>Navicula confervacea</i> <i>Navicula minima</i> <i>Nitzschia amphibia</i> <i>Nitzschia fonticola</i> <i>Nitzschia palea</i> <i>Rhopalodia gibba</i>
Chlorophyta (green algae)		<i>Spirogyra</i> spp.

additions to experimental enclosures in the oligotrophic marsh interior. The calcareous assemblage that existed at low water-column P concentrations (TP = 5 to 7 µg/L) was replaced by a filamentous green algal assemblage at moderately elevated concentrations (TP = 10 to 28 µg/L) and by eutrophic cyanobacteria and diatoms species at even higher concentrations (TP = 42 to 134 µg/L). Taxonomic changes in response to experimental P enrichment were similar to those documented along the marsh gradient (**Figure 3-17**), thereby providing causal evidence that periphyton changes in the marsh were largely a product of P enrichment. Similar conclusions were reached independently by Pan et al. (1997), who also studied diatom changes along marsh and experimental P gradients in WCA-2A.

Whereas increased P loading affects periphyton directly by increasing biomass-specific productivity and favoring species with higher growth rates, other ecological changes caused by P

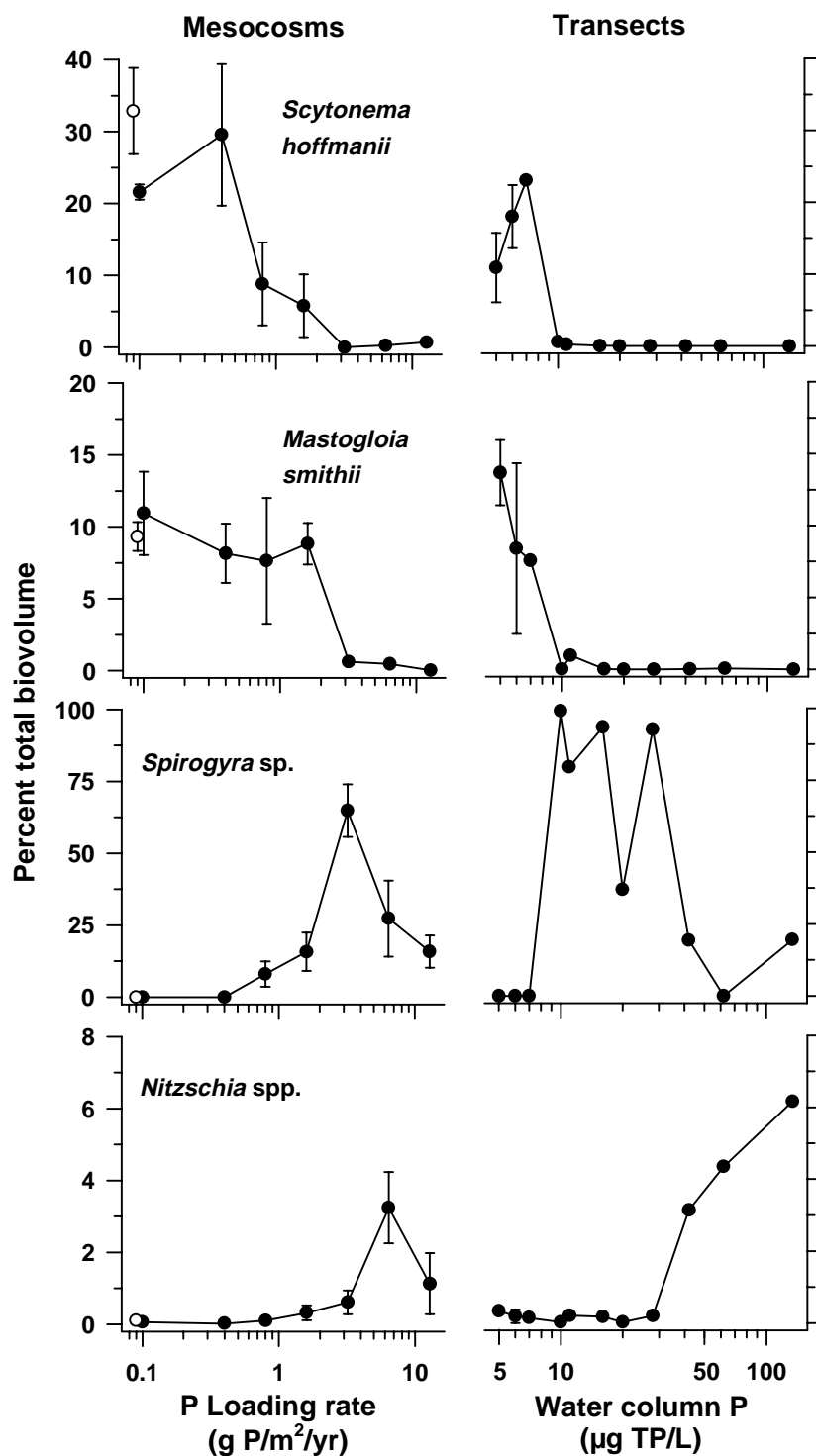


Figure 3-17. Changes in the relative abundance (percent of total algal biovolume) of dominant algal taxa in experimental mesocosm enclosures dosed weekly with different P loads (left panels) and along an enrichment gradient (right panels) in the same marsh (WCA-2A). From McCormick & O'Dell (1996).

enrichment act to reduce periphyton abundance and its contribution to marsh primary productivity in enriched areas. One of the most dramatic effects of P enrichment in the Everglades is to increase the growth and coverage of emergent macrophytes, particularly cattail. Dense macrophyte stands dominate enriched areas of the marsh and reduce light penetration to levels that inhibit periphyton photosynthesis (Grimshaw et al., 1997). Consequently, areal periphyton productivity is considerably lower in enriched areas of the marsh compared with oligotrophic areas (McCormick et al., 1998). These investigators found that productivity in enriched open-water habitats in WCA-2A equaled or exceeded that in oligotrophic open waters (sloughs and wet prairies). However, open water accounted for less than 4% of areal coverage in the enriched marsh compared with 30% in oligotrophic areas of WCA-2A. Periphyton productivity was negligible in the cattail stands that covered more than 90% of the enriched marsh. Consequently, habitat-weighted periphyton productivity in enriched areas of the marsh averaged six-fold lower than in oligotrophic areas during the wet and 30-fold lower during dry seasons (**Figure 3-18**). Independent measurements of aquatic community metabolism also have found extremely low submerged (including periphyton) productivity in enriched areas (Belanger et al., 1989; McCormick et al., 1997).

Periphyton responses to P enrichment appear to be greatest at relatively low water-column P concentrations, and available evidence suggests a shift away from P limitation in highly enriched areas of the marsh. The relationship between periphyton species composition and P in WCA-2A was strongest in areas of the marsh where water-column TP was $< 30 \mu\text{g/L}$ and mass N:P ratios exceeded 50:1 (McCormick et al., 1996). In this same study, enrichment bioassays indicated that limitation by nutrients other than P, particularly N, occurred periodically at sites with higher TP concentrations. Similarly, Vymazal et al. (1994) documented higher periphyton biomass in marsh plots fertilized with both N and P than in those fertilized with P alone. This shift from P to N limitation may explain why experimental P-enrichment studies have reproduced periphyton species changes observed in the marsh at low (e.g., $<30 \mu\text{g/L}$) water-column TP concentrations, but fail to reproduce changes that occur at much higher concentrations (McCormick & O'Dell, 1996).

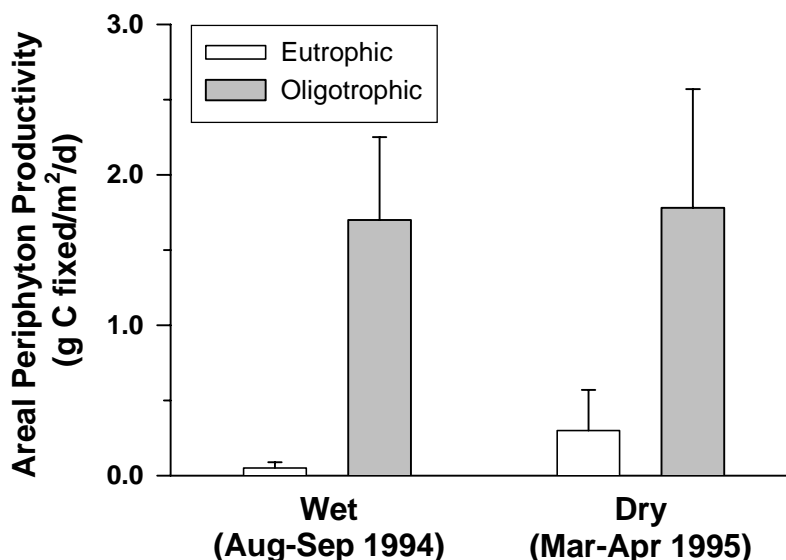


Figure 3-18. Areal periphyton productivity in oligotrophic and enriched areas of WCA-2A during the wet and dry seasons of 1994-1995. Values are means ($\pm 1\text{SE}$) of $n=2$ sampling locations in each area and are habitat-weighted to account for shifts in the areal coverage of different vegetative habitats caused by enrichment. See McCormick et al. (1998) for details.

Community Metabolism and Dissolved Oxygen Concentrations

Phosphorus enrichment causes a shift in the balance between autotrophy and heterotrophy as a result of contrasting effects on periphyton productivity and microbial respiration. Rates of aquatic primary productivity (P) and respiration (R) are approximately balanced (P:R ratio = 1) across the diel cycle in oligotrophic sloughs throughout the Everglades (Belanger et al., 1989; McCormick et al., 1997). In contrast, respiration rates exceed productivity by a considerable margin (P:R ratio \ll 1) at enriched locations. This change is related primarily to a reduction in periphyton productivity coupled with increased detrital inputs that stimulate microbial respiration (e.g., Belanger et al., 1989).

The shift from autotrophy to heterotrophy with P enrichment, in turn, affects dissolved oxygen (DO) concentrations in enriched areas of the marsh. For example, DO concentrations at an enriched site in WCA-2A rarely exceeded 2 mg/L compared with concentrations as high as 12 mg/L at reference locations (**Figure 3-19a**) (McCormick et al., 1997). Depressed water-column DO concentrations have been documented at several enriched marsh locations in WCA-2A and the Refuge and confirmed in experimental P-enrichment studies (McCormick & Laing, in review). Declines in DO along marsh P gradients were steepest within a range of water-column TP concentrations roughly between 10 and 30 $\mu\text{g/L}$ (**Figure 3-19b**). Lower DO in enriched areas of the marsh are associated with other changes including an increase in anaerobic microbial processes and a shift in invertebrate species composition toward species tolerant of low DO as described elsewhere in this chapter.

Marsh Vegetation

Available evidence indicates that vegetation patterns in the Everglades have been affected by P enrichment. As for periphyton, enrichment initially stimulates the growth of existing oligotrophic vegetation as evidenced by increased plant P content, photosynthesis and biomass production. Persistent enrichment and/or enrichment above certain concentrations eventually produces a shift in vegetation composition toward species better adapted to rapid growth and expansion under conditions of high P availability. Current understanding of the progression of vegetation changes associated with P enrichment is based on: (1) life-history strategies of dominant species; (2) patterns of physiological, population, and community change along marsh P gradients; and (3) experimental studies that have documented macrophyte responses to controlled-P enrichment. Unfortunately, experimental data are less conclusive than for periphyton, because macrophyte responses take longer to occur and few experiments have been conducted long enough to document noticeable shifts in macrophyte species composition. Current models suggest that time lags between P enrichment and vegetation responses may be several years (e.g., Walker & Kadlec, 1996). Thus, much of the evidence for P-related changes in Everglades vegetation is based on correlative and observational evidence from field studies, have been corroborated by small-scale greenhouse and field experiments that provide mechanistic explanations (e.g., differential changes in germination and growth rates) for these changes.

P-limited nature of Everglades macrophytes

It is generally accepted that macrophyte communities in the Everglades are P-limited. However, with the exception of sawgrass and cattail, macrophytes have received scant study, other than analyses of their distribution and abundance. Studies indicate that sawgrass is adapted to the low-P conditions indicative of the pristine Everglades (Steward & Ornes, 1975b; Steward & Ornes, 1983). During field and greenhouse manipulations, sawgrass responded to P enrichment either by increasing the rate of growth or P

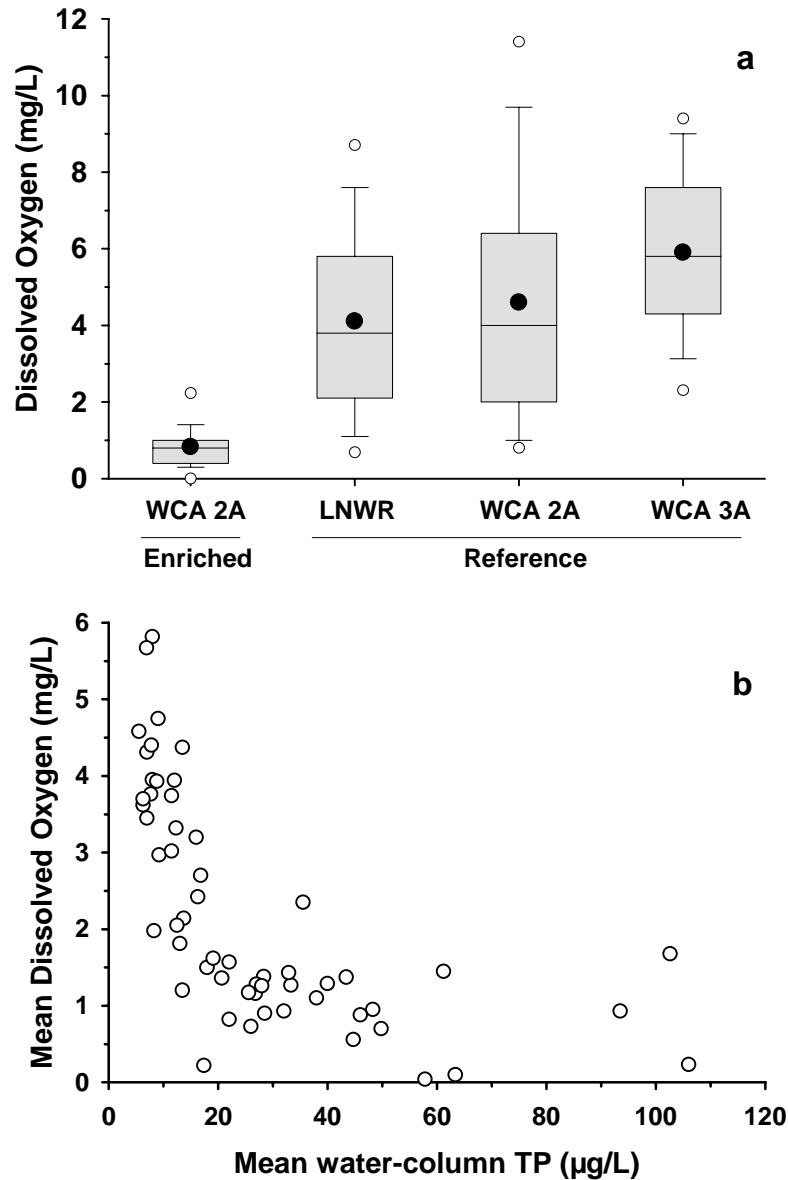


Figure 3-19. **a.** Average water-column dissolved oxygen concentrations and ranges at three reference marsh stations in the WCAs and an enriched marsh station in WCA-2A based on periodic diel sampling between 1979 and 1985 (from McCormick et al., 1997). The top, mid-line, and bottom of each box represents the 75th, 50th (median), and 25th percentiles of data, respectively; the vertical lines represent the 10th and 90th percentiles, and the open circles are the 5th and 90th percentiles; large closed circle is the arithmetic mean. **b.** Changes in mean daily water-column DO at 13 sampling stations along a canal P gradient in WCA-2A during 5 sampling periods between 1995 and 1998. Each point is the mean value for a single station during a single period. Each period encompassed 3 to 4 successive diel cycles with measurements taken at 15-30 minute intervals using Hydrolab Datasondes[®] suspended at mid-depth in the water-column. See McCormick and Laing (in review) for further details.

uptake (Steward & Ornes, 1975a; Steward & Ornes, 1983; Craft et al., 1995; Miao et al., 1997; Daoust & Childers, in review). Furthermore, additions of N alone had no effect on sawgrass or cattail growth under low- P conditions (Steward & Ornes, 1983; Craft et al., 1995). Recent experimental evidence in the Park (Daoust & Childers 1998) has shown that other native vegetation associations such as wet prairie communities are limited by P as well.

Changes in sawgrass habitats

In the Everglades, sawgrass displays life-history characteristics indicative of plants adapted to low-nutrient environments (Davis, 1989; Davis, 1994; Miao & Sklar, 1998). Compared with cattail, sawgrass plants display slow growth, extended life cycles, low reproductive yield, and an inability to alter biomass allocation (e.g., storage vs. photosynthetic tissues) in response to changes in the resource environment (**Table 3-2**). As expected in a P-limited ecosystem, the P concentration of sawgrass tissue increases with increases in soil and water-column P concentrations (**Figure 3-20**) (Koch & Reddy, 1992; Craft & Richardson, 1997; Miao & Sklar, 1998; Richardson et al., 1997). This P accumulation is associated with increases in plant biomass, P storage, and annual leaf production and turnover rates along a P gradient in WCA-2A (Davis, 1989; Craft & Richardson, 1997; Miao & Sklar, 1998). Population dynamics also are affected by P accumulation as indicated by changes in plant density and size, with a higher density of smaller plants in reference areas and lower densities of larger plants in enriched locations (Miao & Sklar, 1998). In addition, P enrichment enhances sawgrass seed production by increasing both the yield and the number of seeds produced (Goslee & Richardson, 1997; Miao & Sklar, 1998).

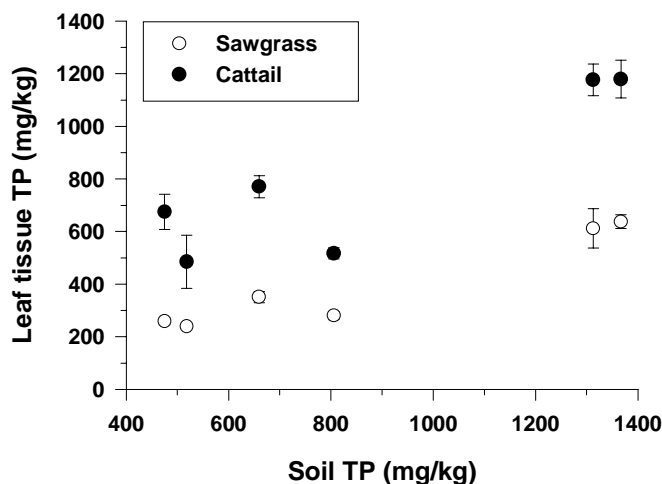


Figure 3-20. Changes in sawgrass and cattail P concentration (leaf tissue TP) along a soil P gradient downstream of the S10s in WCA-2A. Adapted from Miao & Debusk (in press).

Changes in slough/wet prairie vegetation

Sloughs and wet prairies harbor much of the biodiversity and secondary production of the Everglades and provide critical foraging habitats for top predators, such as wading birds (Belanger et al., 1989; Hoffman et al., 1994). Available evidence indicates that these habitats are particularly sensitive to P enrichment and are replaced by cattail stands in enriched areas of the marsh. This transition represents a fundamental shift in both community structure and function. Changes occur in two stages: (1) alteration of existing vegetation; and (2) invasion by cattails.

Table 3-2. Summary of differences in life history characteristics between sawgrass and cattail based on various sources (Davis 1989, 1991, 1994; Chanton et al. 1993; Miao and Sklar, 1998; Miao and DeBusk, in press; Stewart et al., 1997; Goslee and Richardson, 1997).

	Sawgrass	Cattail
1. Growth		
Leaf turnover rate (g/g/yr)	low (1.99 - 2.57)	high (3.64 - 5.17)
Leaf production (g/m ² /yr)	low (802 - 2028)	high (1077 - 3035)
Annual leaf biomass (g)	slow (403 - 803)	fast (296 - 587)
2. Physiology		
Photosynthetic rate (μmol/m ² /s)	low (10 - 17)	high (18 - 27)
Stomatal conductance (μmol/m ² /s)	low (170 - 300)	high (220 - 500)
Leaf vs. root biomass allocation	inflexible	flexible
3. Reproduction		
Seed yield (g)	low (4 - 7)	high (8 - 15)
Seed number (mg)	low (8 - 35 x 10 ²)	high (1.8 - 3.5 x 10 ⁵)
Seed size	large (2.3 - 3.9)	small (0.04 - 0.06)
Flowering	March-May	January-February
Fruiting	June-August	April-June
Timing of dispersal	July-August	May-July
4. Germination		
Min. days required for germination	14-22 days	2-7 days
Germination (%)	low (1 - 40)	high (15 - 100)
Germination duration	>6 months	2-3 weeks
5. Morphology & anatomy		
Leaf	narrow & tough	wide & spongy
Leaf cuticle	well-developed	poor
Air space in leaves	small	large
Gas transport	diffusion	bulk flow ventilation

Slough habitats in the northern Everglades are characterized by *Nymphaea odorata* and *Utricularia purpurea*. These habitats intermix with wet prairies, which are typically dominated by *Eleocharis* spp. Changes in species composition and biomass and the gradual disappearance of these communities have been documented along an enrichment gradient downstream of the S10 structures in WCA-2A. Satellite imagery and aerial photography indicated a decline in open-water habitats and a corresponding increase in cattail coverage in enriched areas of the marsh (Rutchey & Vilchek, 1994; Rutchey & Vilchek, in press). A recent study (Tetra Tech, 1998) using computer-processed, scanned aerial photography reported an increase in open water areas between 1991 and 1995 in WCA-2A. However, the research was narrowly focused and limited to areas that exhibited spectral returns similar to the deepwater rim canals and much of the increase involved new and expanded airboat trails. Thus, the study did not address changes in coverage of sloughs and wet prairie habitats. The process of slough enrichment and replacement by cattail indicated by remote sensing is supported by ground-based sampling methods (McCormick et al., in preparation). The abundance of macrophyte species was estimated in 27 sloughs downstream of the S10 structures by measuring presence-absence of each species in 25 equally spaced 1-m² plots along a 50-m fixed transect at each site. This study documented changes in dominant slough vegetation and encroachment of these habitats by cattail as far as 7 km downstream of the structures where soil TP concentrations averaged between 400 and 600 mg/kg (Figure 3-21). Whereas *Eleocharis* declined in response to increased soil P, *Nymphaea* was stimulated by enrichment and was dominant in slightly enriched sloughs. Increased occurrence of cattail in sloughs was associated with a

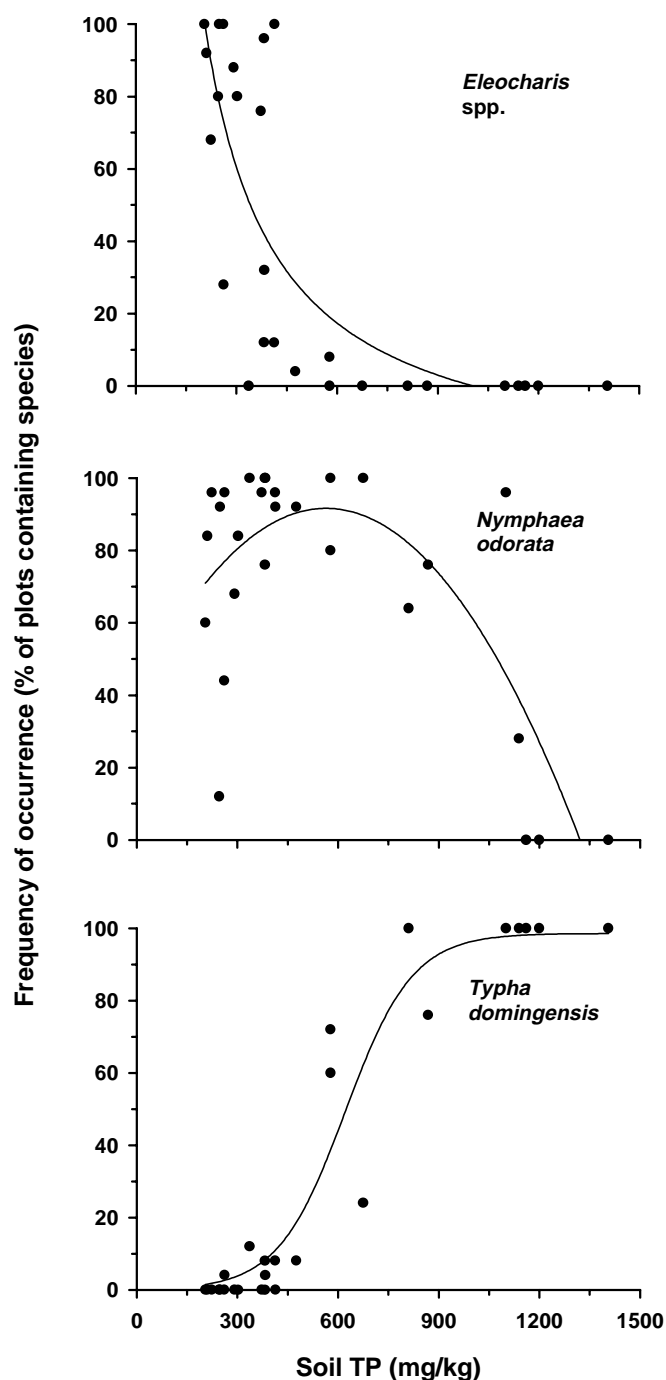


Figure 3-21. Changes in dominance (frequency of occurrence in 25 1-m² plots at each site) of common macrophyte species in sloughs as a function of soil TP downstream of the S10s in WCA-2A in 1997. Lines drawn to show general trends with increasing enrichment.

decline in *Nymphaea*, probably as a result of increased shading of the water surface. These findings are consistent with those of Vaithianathan et al. (1995), who documented a decline in slough habitats along this same enrichment gradient and the loss of sensitive taxa such as *Eleocharis* at locations where soil TP exceeded 700 mg kg⁻¹. Patterns of response to P enrichment in slough-wet prairie communities in the southern Everglades are somewhat different from those in the northern Everglades. In a field dosing experiment in Shark Slough, Scheidt et al. (1989) documented a shift from an *Eleocharis-Utricularia* marsh to one dominated by *Sagittaria* sp. and *Panicum* sp. at a mean water-column SRP of 33 µg/L (5.5 times background concentrations of 6 µg/L).

Vegetation changes documented along marsh enrichment gradients are supported by experimental P-enrichment studies. Phosphorus additions to slough plots at a loading rate of 4.8 g P/m²/yr resulted in the loss of the existing *Utricularia*-periphyton community (Craft et al., 1995). Similar results were obtained in slough P enrichment studies in WCA-2A and WCA-3B (Steward and Ornes, 1975a; McCormick and O'Dell, 1996; Newman, unpublished data). In the WCA-2A study, *Nymphaea* P accumulation and leaf growth rates increased in response to loads of 6.4 to 12.8 g P/m²/yr within two years, and to loads of 3.2 g P/m²/yr within three years (Miao et al., in preparation). Similarly, experimental P enrichment of an *Eleocharis* wet prairie in the Park resulted in an increase in net aboveground primary productivity and an accelerated rate of biomass turnover (Daoust, 1998).

Cattail invasion rarely has been documented in slough enrichment experiments. As discussed below, this lack of experimental confirmation of gradient trends may relate to the relatively short duration of these enrichment studies. For example, cattail became established in P-enriched dosing channels in the Park only after several years following the cessation of dosing (R. Jones, Florida International University, personal communication). Enrichment of slough plots in WCA-2B with P also resulted in cattail invasion after existing vegetation had been cleared (Richardson et al., 1995). The preferential pattern of cattail encroachment into open-water habitats is consistent with the life history characteristics of this species and its response to P enrichment, as determined by experimentation discussed below.

Changes in cattail distribution and its relationship to P enrichment

The southern cattail, *Typha domingensis*, is found in wetlands in warmer climates and is considered to be a natural component of the Everglades ecosystem. In oligotrophic areas of the marsh, this species occurs largely as scattered diffuse stands (Davis, 1994). However, a rapid increase in the spatial distribution of cattail has been documented across the Everglades in recent decades (Rutchey & Vilchek, 1994; Jensen et al. 1995; Newman et al., 1998; Rutchey & Vilchek, in press). The most dramatic expansion has occurred in WCA-2A, where the total area of the landscape containing > 90% cattail coverage increased from 422 ha in 1991 to 1,646 ha in 1995 (**Figure 3-22**) (Rutchey & Vilchek, in press), and the yearly invasion rate of cattail increased from 1% in 1973 to 4% by 1987 (Wu et al., 1997).

Several studies have shown that cattail expansion in the Everglades is associated with both fertile and disturbed environments (Davis, 1991; Urban et al., 1993; Craft & Richardson, 1997; Richardson et al. 1997; Miao & Sklar, 1998; Miao & DeBusk, in press), and that a combination of elevated nutrients and increased flooding will allow cattail to outcompete sawgrass and slough vegetation (Newman et al., 1996). Vegetation and soils analyses along nutrient gradients show that cattail populations are extensive in areas with elevated soil P concentrations (DeBusk et al., 1994; Craft & Richardson, 1997; Doren et al., 1997; Newman et al., 1997; Miao & DeBusk, in press; McCormick et al., in preparation). Using a Markov

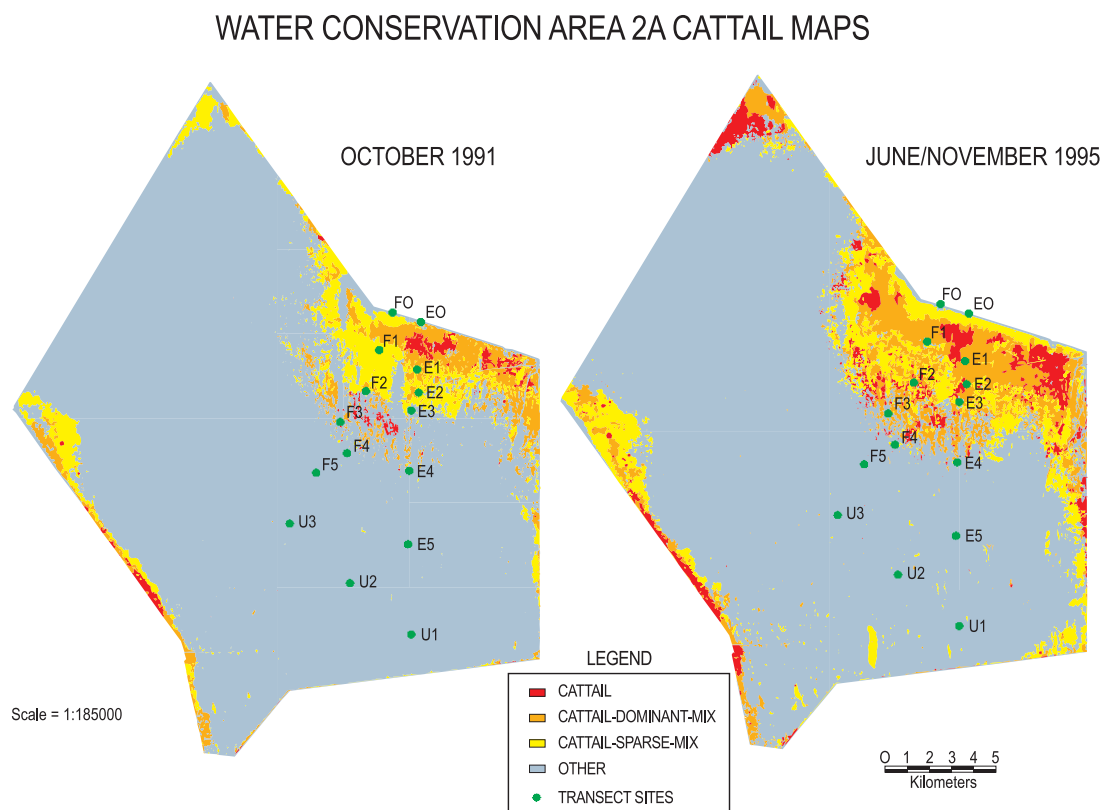


Figure 3-22. Changes in the coverage of cattail within WCA-2A between 1991 and 1995. Coverage estimates are based on ground-truthed aerial photography as described by Rutchey and Vilchek (in press).

transition probability model to quantify the dynamics of the rapid cattail expansion in WCA-2A, Wu et al. (1997) suggested that cattail expansion is accelerated at soil TP concentrations >650 mg/kg. Furthermore, due to high P concentrations already present in soils downstream of the S10 and S7 structures, a more recent District model, the Everglades Landscape Vegetation Model, predicts that cattail will continue to expand and occupy approximately 30% of WCA-2A in the next 20 years even in the absence of continued P inputs. These predictions are consistent with modeling efforts by Walker & Kadlec (1996) that indicate a lag between P enrichment and cattail invasion.

Field experiments support a close relationship between cattail growth and expansion and P enrichment. Cattail plants transplanted to enriched and unenriched sites and allowed to grow for seven months exhibited significantly different growth responses. Plants grown at the enriched site had approximately 170% greater relative growth rate and produced over 10-fold more biomass than those grown at the unenriched site (Miao & DeBusk, in press) (**Figure 3-23**). After two years, the transplanted cattail plants expanded and filled in all open areas (approximately 560 m^2) at the enriched site, while no expansion occurred at the unenriched site.

Factors other than P may influence cattail expansion in some areas. For example, cattail expansion is correlated with hydrologic changes in Holey Land and with severe muck fires in Rotenberger (Newman

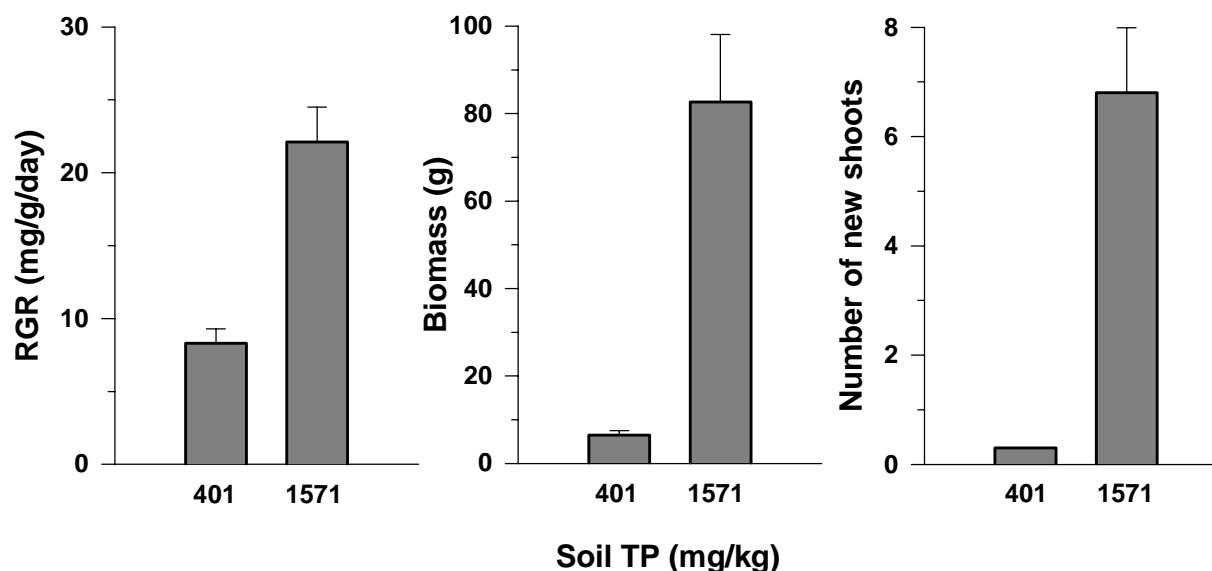


Figure 3-23. Relative regrowth rate (RGR), biomass production, and the number of new shoots produced by cattail plants transplanted to enriched and unenriched sites in WCA-2A. Bars are means (+ 1SE) of measurements taken from 12 plants at each site. Adapted from Miao & Debusk (in press).

et al., 1998). However, soils in these areas also were high in P, on a volumetric basis, prior to cattail expansion. When soil TP is corrected for bulk density and soil depth, both Holey Land and Rotenberger have elevated soil TP compared to other areas of the Everglades. This suggests that both areas have sufficient P to support rapid cattail expansion, which may have contributed to a greater initial growth rate for cattail in Holey Land relative to other regions of the northern Everglades. The total extent of cattail coverage in Holey Land increased 12-fold from 1991 to 1995 (a conservative estimate) compared with a 1.7-fold increase in WCA-2A during this same period (**Figure 3-24**). Thus, rapid cattail expansion appears contingent upon high P availability. However, while developing this hypothesis, it is recognized that the form of P in the soils will influence its bioavailability. Holey Land soils have inorganic P values two-fold higher than any other northern Everglades soils. Also, inorganic P is correlated positively with cattail cover. Inorganic P is taken up directly by higher plants and is readily available to support growth (Marschner, 1986). Organic P, the primary form of P stored in Everglades soils, must be mineralized to inorganic P before it can be utilized for growth. Elevated levels of inorganic P also are associated with enriched, cattail-dominated areas of WCA-2A (DeBusk et al., 1994).

Cattail is characterized by high growth rates, a short life cycle, high reproductive output, and other traits that confer a competitive advantage under enriched conditions (**Table 3-2**). For example, higher photosynthetic rates, an indicator of potential growth rate, may allow cattail to outcompete sawgrass under enriched conditions. Although the two species exhibited similar photosynthesis rates in unenriched areas, where soil TP averaged near 450 mg/kg, rates for cattail were approximately 47% greater than for sawgrass in areas where soil TP concentrations exceeded 500 mg/kg (Miao & DeBusk, in press). Higher photosynthetic rates were associated with greater leaf production by cattail plants compared with sawgrass in enriched areas (Davis, 1989).

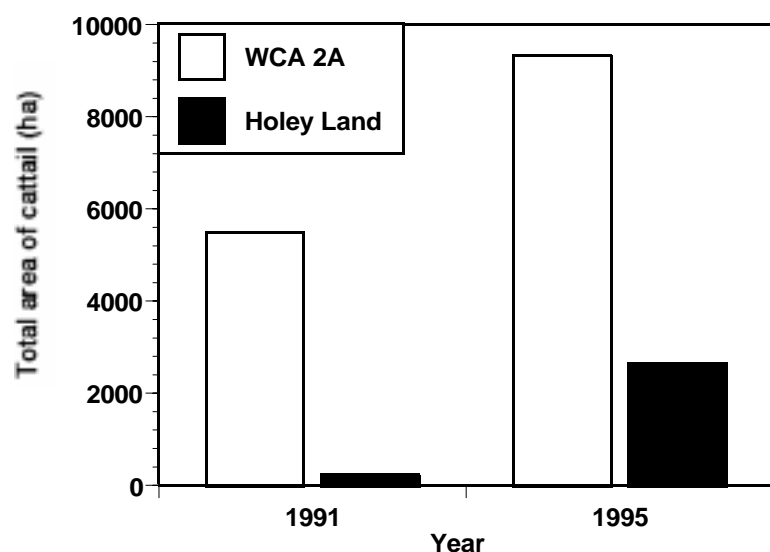


Figure 3-24. Increases in total cattail coverage over time in Holey Land and WCA-2A. Holey Land data collected using aerial point sampling (source: Florida Game and Freshwater Fish Commission). WCA-2A data collected using aerial photointerpretation (Rutchev and Vilchek, in press).

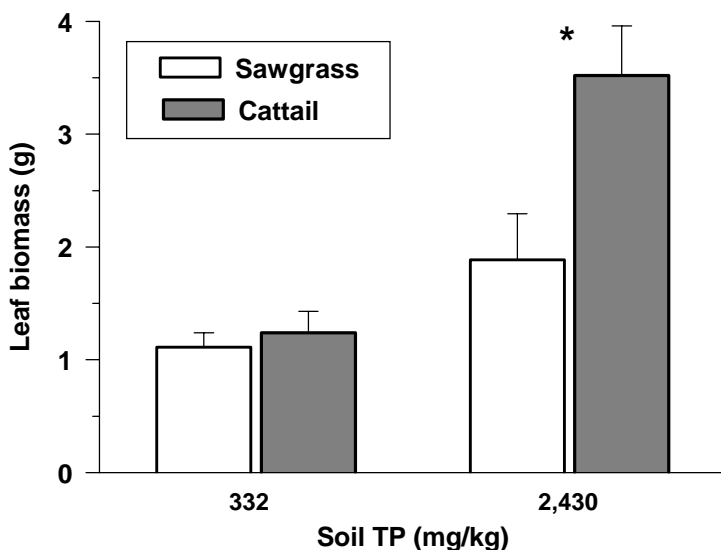


Figure 3-25. Leaf regrowth rate (biomass produced) following leaf removal for cattail and sawgrass plants grown in enriched and unenriched soil. Bars are means (\pm 1SE) of measurements taken from 25 plants from each site. Adapted from Miao & Debusk (in press). Asterisk above bars shows significant difference between species ($P < 0.05$, ANOVA).

Experimental studies also indicate that cattail is a competitively superior species under enriched conditions. For example, the rate of regrowth following leaf removal (as might be caused by fire) was similar for cattail and sawgrass grown under unenriched conditions, but was approximately 75% faster for cattail when the two species were grown in P-enriched soils (**Figure 3-25**) (Miao & DeBusk, in press). Findings such as these indicate the ability of cattail to recover and expand more quickly than sawgrass following certain types of disturbance (e.g., surface fires) in P-enriched areas. The relationship between P enrichment and cattail expansion has been clouded by the results of field enrichment studies conducted by the Duke Wetlands Center and the District, which have not found P enrichment to lead to cattail establishment in sloughs. These studies are relatively short-term (< five years) compared to the history of enrichment in the Everglades (>30 years) and may not span a sufficient timeframe. This raises the question of whether there is a lag time between enrichment and establishment and the factors (e.g., seed dispersal, marsh drying) that might contribute to this lag.

Like most clonal plants, cattail can spread by two methods: (1) seed dispersal and germination; and (2) vegetative growth via rhizomes. Whereas expansion via vegetative growth is slow and requires an existing vegetation stand, seed dispersal and germination allow for new stands to become established at distant locations. High seed production and wind dispersal are

characteristics of cattail that should enhance this species' ability to invade new locations (McNaughton, 1966; Grace & Wetzel, 1981; Wilcox et al., 1985; Grace, 1987; Stewart et al., 1997). Initial invasion of a new location is dependent upon seed availability followed by successful germination and seedling survival. Densities of viable cattail seeds in the surface soils of the northern and central Everglades generally are quite low (Van der Valk & Rosburg, 1997; Miao et al., in review), and cattail seed banks are restricted largely to areas where cattail stands are the dominant vegetation (Van der Valk & Rosburg, 1997). Even in areas with viable seed banks, cattail establishment appears to be quite slow under low P conditions due to reduced seed germination after dispersal and low seedling survival. Greenhouse studies have shown that while cattail seeds germinate rather quickly (within two to five days) (Stewart et al., 1997; Lorenzen et al., in press), initial seedling growth is slower than for sawgrass seedlings, particularly under low-nutrient conditions (Miao unpublished data; Goslee & Richardson 1997). The survival and growth of cattail seedlings was most successful when grown under high soil nutrient concentrations and saturated (as opposed to flooded) soils (Miao et al., in review; Miao & Newman, unpublished data). Under low soil nutrient concentrations and flooded soil conditions, cattail seedlings exhibit high mortality (Miao, unpublished data). Thus, while established cattail stands are extremely tolerant of a wide range of environmental conditions, the successful colonization of new locations via seed dispersal appears dependent upon specific hydrologic and nutrient conditions.

Lower trophic levels

Invertebrate responses to P enrichment appear to be driven primarily by P-induced changes in: (1) the quantity and quality of different food resources; (2) water-column DO; and (3) the availability of suitable substrata as habitat. Much of the existing evidence for invertebrate changes in response to P enrichment have come from transect studies along the water quality gradient in WCA-2A (Rader & Richardson 1994). Ongoing dosing studies being conducted by the District, Duke Wetlands Center, and Florida International University in WCA-2A, the Refuge, and the Park will provide additional experimental evidence of P-related changes.

Rader & Richardson (1994) sampled invertebrate assemblages in open-water habitats along an enrichment gradient in WCA-2A produced by canal inflows through the S10 structures. Sampling was conducted on six dates between 1990 and 1991 using sweep nets (mesh size 2.0 to 2.5 mm) and sediment cores. Invertebrate species richness was highest at the most enriched sites, while Shannon's diversity was highest at sites exposed to intermediate levels of enrichment. Species shifts were observed along the gradient, although most major taxonomic groups reached their highest densities at enriched sites. No shift in the functional composition of the assemblage was noted along the gradient. Sampling was limited to a single habitat (open-water), which is common in unenriched areas but extremely sparse in enriched areas (see McCormick et al., 1998). Therefore, conclusions concerning areal changes in invertebrate densities and production in response to enrichment are limited. Available evidence suggests that invertebrate densities and species richness may be lower in macrophyte stands (Terczak, 1980; Davis, 1994), which account for more than 90% of areal coverage in enriched areas of WCA-2A.

District investigators (unpublished data) collected invertebrates using sweep nets (0.35 mm mesh size) on a quarterly basis during 1994 and 1995 along this same gradient. Rather than concentrating solely on open-water habitats, these investigators sampled on a habitat-weighted basis to account for changes in vegetation coverage along the gradient. No changes in macroinvertebrate density, species richness, or diversity occurred along the gradient. However, significant changes in taxonomic and functional composition were detected. A shift in species composition at enriched sites toward dominance by taxa

tolerant of low DO was consistent with substantially lower DO concentrations at these sites compared with oligotrophic areas. Shifts in functional composition toward increased proportional abundance of detritivores and decreased grazers at enriched sites were consistent with a reduction in open-water habitats and periphyton biomass in these areas. Differences in conclusions between this study and Rader and Richardson (1994) may be related to the finer mesh size and habitat-weighted sampling employed in the District study.

Few experiments have investigated the relationship between invertebrate abundance and composition and P enrichment in the Everglades. The macroinvertebrate assemblage was sampled on artificial substrata (Hester-Dendy samplers) in flume dosing channels that had been exposed to different P loads for several years (Zahina & Richardson, 1997). Invertebrate colonization of these substrata was extremely variable apparently due to pronounced differences in vegetation between replicate channels. Consequently, few discernible trends in invertebrate density and taxonomic or functional composition were detected. However, there was weak evidence that a few taxonomic groups (oligochaetes and ostracods) responded positively to enrichment in a manner similar to that documented along P enrichment gradients in the marsh (Rader & Richardson, 1994). Further gradient and experimental studies are required to establish invertebrate changes induced by P enrichment and the mechanisms (e.g., oxygen depletion, changes in food base) underlying such responses.

Potential impacts on higher trophic levels

There are few data on the effects of nutrient enrichment on fish communities in the Everglades. In WCA-2A, Rader and Richardson (1994) found similar fish species composition between enriched and unenriched sites, but fish densities were two- to three-fold higher in enriched areas. Likewise, Turner et al. (in press) found that fish biomass at enriched sites in WCA-2A and the Park averaged over 1 g/m² and were consistently higher than at unenriched sites. These investigators concluded that P enrichment was an important factor contributing to changes in animal biomass from the reference condition. Similar biomass patterns were observed in the Okefenokee Swamp, where local nutrient enrichment from a wading bird colony resulted in increased fish biomass (Oliver & Schoenberg, 1989).

Nutrient enrichment can affect bird communities indirectly through effects on their food and through effects on vegetation structure, which provides foraging and nesting substrate. A generalization that emerges from numerous studies on bird-habitat relationships is that bird density or species richness is related positively to vegetation density, volume, or biomass (Gough et al., 1994). In freshwater marshes, maximum species richness was attained when the ratio of open water to vegetated wetlands reached 50:50 (Weller & Spatcher, 1965). A statistical analysis of wading bird abundance in relation to vegetation in the northern Everglades indicated that the relationship between bird abundance and cattail area was positive at low to moderate cattail coverage and then decreased (Bancroft et al., in review). Likewise, Hoffman et al. (1994) found that wading birds avoided areas with dense macrophyte cover when feeding.

Modeling to Understand and Predict the Ecological Effects of P Enrichment

This chapter has summarized data and findings on a wide range of potential effects of P enrichment on the Everglades ecosystem. These processes interact at a number of spatial and temporal

scales and, therefore, become difficult to summarize at the ecosystem level. The Everglades encompasses a mosaic of habitats spread across a large spatial extent. Changes in some ecosystem characteristics encompass decadal time scales. Yet, the current quantitative understanding of the Everglades comes from comparatively limited spatial and temporal studies. Dynamic spatial simulation models are potentially useful tools for evaluating the landscape response to P enrichment over large temporal and spatial scales.

Several spatial simulation modeling tools have been developed to investigate various aspects of P enrichment of the system. These models encompass a range of spatial and temporal scales, with varying levels of ecological and computational complexity. While all of the models address the relationship between nutrient loading and resulting water quality (Act 4(e)3) and biological responses, they incorporate different assumptions. Thus, evaluation of their different outputs will enhance understanding of Everglades P dynamics. These models are presented below and described in more detail in the following discussion.

- **The Everglades Water Quality Model (EWQM)** was developed to evaluate the relationship between P loads and concentrations in the Everglades Protection Area (EPA). It uses a 10.4 km² grid cell size (642 cells plus 19 canal segments) and a monthly time step, aggregating the P dynamics associated with plants, water, and soils into an empirically derived, net settling (loss) rate of TP from the water-column.
- **The Everglades Phosphorus and Hydrology (EPH) model** was developed to evaluate the relationship between P loads and concentrations in the Everglades Protection Area (EPA). It is similar in intent to the EWQM, but operates at a coarser spatial scale of resolution (20 cells). The EPH aggregates the P dynamics associated with plants, water, and soils into an empirically derived, net settling (loss) rate of TP from the water-column.
- **The Sawgrass Cattail (SAWCAT) model**, at a 400 m² grid cell resolution, uses empirical correlations between soil TP and cattail distribution to calculate probabilities of cattail expansion. It estimates increases in soil TP concentrations, and concomitant cattail expansion from historical trends in WCA-2A.
- **The Everglades Phosphorus Gradient Model (EPGM)**, is a spatially aggregated mass balance model that predicts the effects of STA P loads on water and soil P concentrations and resulting growth of cattail communities. The model is similar in intent to SAWCAT and was developed by Walker and Kadlec (1996).
- **The Everglades Landscape Vegetation Model (ELVM)** predicts vegetation succession within WCA-2A at a 0.01 km² grid cell scale using daily time steps. It uses empirically based soil TP algorithms similar to SAWCAT but incorporates the mechanisms of macrophyte growth and succession in response to changes in available nutrients, hydrology, and disturbances.
- **The Everglades Landscape Model (ELM)** simulates interactions among hydrology (and hydrologic management of the canal network), chemistry, and biology of the marsh systems across the EPA and Big Cypress at a 1.0 km², or smaller, scale and a variable (0.01 to 0.5 day) time step. The ELM incorporates the principal mechanisms associated with dynamic hydrology, N and P cycling in the water-column and soil, and growth/succession of periphyton and macrophytes. This provides a synthesis of changes in ecosystem processes in response to changing environmental inputs. The ELVM and ELM are further described in **Chapter 2**,

indicating the importance of considering the combined influence of all ecological processes on landscape/ecosystem development.

Everglades Water Quality Model

The EWQM (Limno-Tech, 1995) simulates P transport in the EPA, which includes all WCAs and part of the Park. Canals within the modeling area are also included in the simulation. Various factors including P loading (structural input from EAA and non-point source atmospheric deposition), hydrologic loading, and first-order P settling rate, are used in calculating the P concentrations with a mass balance approach. Hydrologic information for the model, such as water flow and ponding depth, is obtained from the South Florida Water Management Model (SFWMM). In determining P removal, a first-order settling rate is used to describe the net effect of more complicated P removal and cycling processes, which include sedimentation/resuspension, adsorption/desorption, plant uptake and release, as well as other P-related physical and chemical processes. This simplifies the simulation of the net effect while the mechanisms of the processes can be further investigated and incorporated into this and other models later. Model output provides spatial and temporal predictions of water-column P concentrations in the EPA.

Section 4.(e).3 of the Act requests information that can help define “Other relationship between waters discharged to, and the resulting water quality in, the Everglades Protection Area.” The EWQM was designed specifically to predict these relationships at a regional scale. Model results so far indicate that P loads from the EAA have a significant effect on water-column P concentration in the EPA, especially in areas adjacent to inflow structures and canals (**Figure 3-26**). Phosphorus concentrations in areas remote from inflow structures and canals are less affected by P loads from the EAA. The model also shows that decreasing the P loads from the EAA can directly reduce the P input into the Park through S12 and S333 structures (**Figure 3-27**).

Although the model typically is used to determine P concentrations in the EPA for given P loads, it also can be used to determine P loading limits when the maximum P concentrations in the EPA are established. For example, if the maximum P concentration that does not result in ecological imbalance is determined to be 10 µg/L, the model can be run in a trial-and-error method with different P loads for each simulation to derive a loading rate to achieve this concentration limit.

Everglades Phosphorus and Hydrology model

This P fate and transport model for the Everglades Protection Area was developed by Tetra Tech, Inc. (1998) for the Sugar Cane Growers Cooperative of Florida. The EPH model divides the modeled area into twenty cells of differing size, half of which are larger than 10,000 hectares (ha.) with the largest close to 47,000 ha. in size; in contrast, the size of the EWQM cells is 1040 ha. Within each cell, the hydrologic processes simulated include precipitation, evapotranspiration, inflow, outflow, and storage. Chemical processes simulated by the EPH model include net P removal to sediments. The EPH also has provisions for calculation of soil-water phosphorus equilibrium partitioning and P remineralization upon drying of wetland soils, but this part of the model code is currently not used. The fate and transport of P throughout the modeled area, therefore, is governed by removal of P to sediments and the hydrologic processes affecting the 20 cells. With regard to the latter, however, model documentation in Tetra Tech, Inc. (1998) suggests that the EPH either ignores the canal system in the Everglades Protection Area, which is capable of carrying water and P to downstream areas rapidly, or represents canals as cells that are larger than the

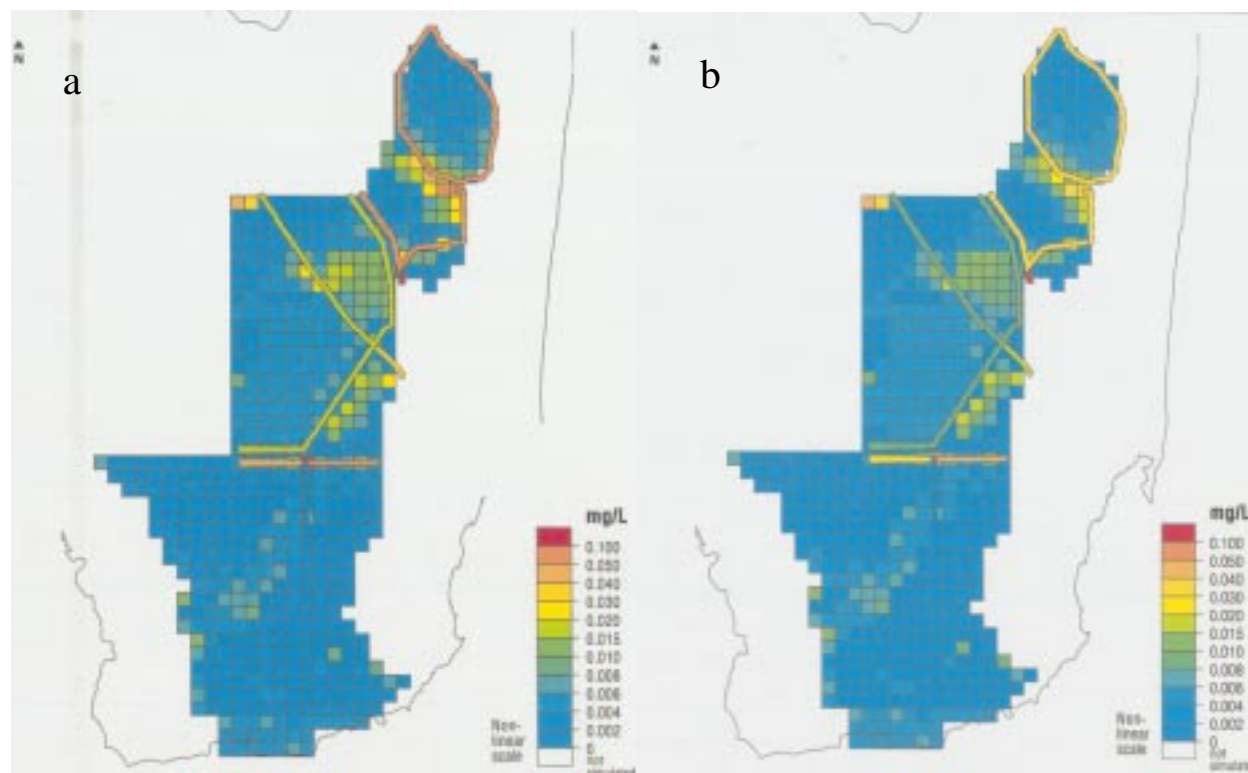


Figure 3-26. Average annual water-column marsh TP concentrations predicted by the Everglades Water Quality Model (EWQM) under: (a) recent (1979-1989) P loading rates from the EAA; and (b) a 50% reduction in EAA loads.

actual canal. For example, the Hillsboro Canal (L-39) at the southern end of Refuge was not modeled as a separate cell but was merged with the area north of the canal, represented by a cell of 11,734 ha (cell 3). Canal L-67, which can move water-column P quickly (relative to sheet flow) to the S-333 and S-12 structures and has a significant impact on the phosphorus loads into the Park, is not modeled as a separate cell. Instead, the canal is combined into EPH model cell numbers 18 and 20, which represent a substantial portion of WCA-3A area. For canals that the EPH does simulate as separate cells, such as the Refuge internal borrow canal and the Miami Canal (represented by cell 1 and 11 respectively), cell areas appear to be larger than the actual area of the canal. For example, cell 11 is defined as a 400 ha cell in the EPH model, whereas the actual area of the canal may be less than 150 ha. The effects of such canal treatment and the use of large cell sizes would lead the EPH model to underestimate the impact of upstream P loads (and reductions thereof) on downstream P concentrations. Specifically, as cell size increases, the ability to predict localized and rapid changes in phosphorus concentration decreases. Furthermore, if simulated canal water flows and sheet water flow are merged into large cells, the rate and amount of P delivered to downstream areas will be decreased. Finally, as cell size increases and canals are included in cells, model calibration and verification exercises become more challenging because point measurements may not be representative of the large, simulated area.

The EPH was used to evaluate three scenarios: (1) the base case (no P reductions); (2) the Act case (includes operation of six STAs and P reductions of 25% by on-farm BMPs); and (3) a modified Act case where one of the STAs (number 3/4) is removed, and BMPs are assumed to reduce P loads by 50%. Under

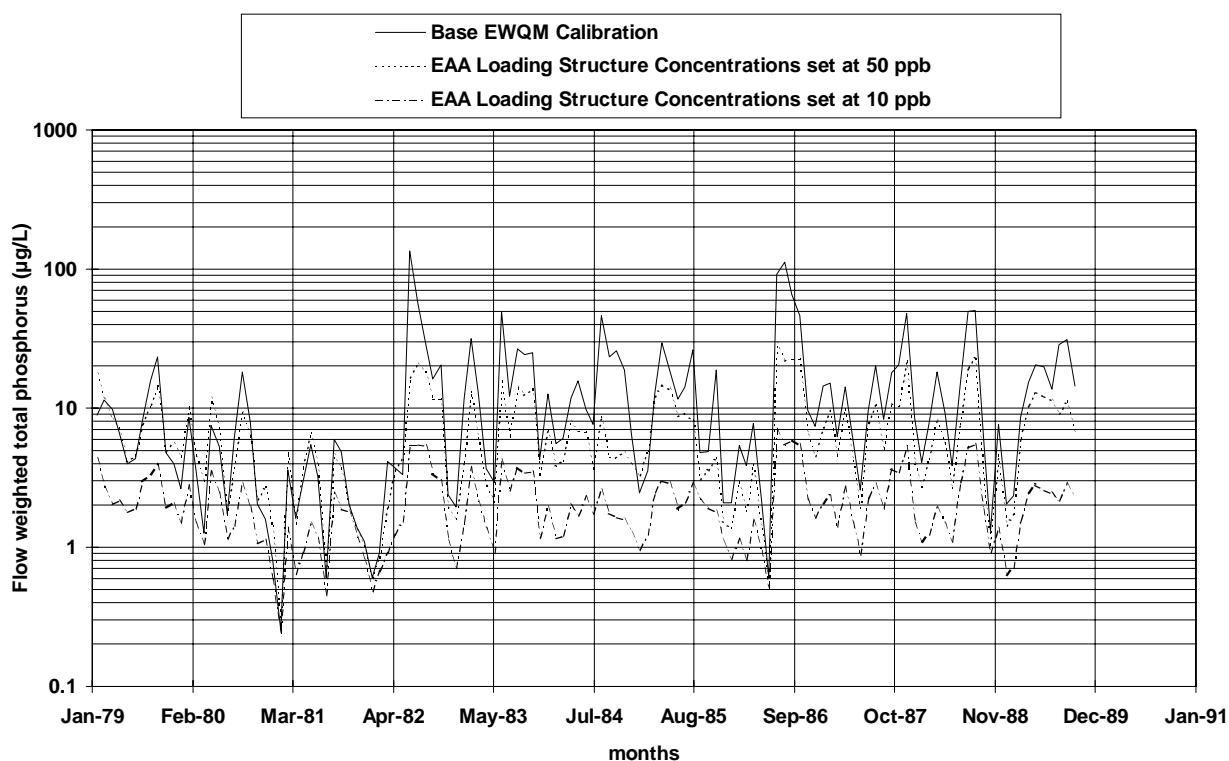


Figure 3-27. Sensitivity of TP concentrations at the S12 structures to P loading rates at EAA structures (S5, S6, S7, S8, and S150) as predicted by the Everglades Water Quality Model (EWQM).

the Act and modified Act case, the EPH predicts decreased P concentrations in areas near EAA discharges, but little impact on P concentrations entering the Park. The EWQM also found that P loads from the EAA have a significant effect on water-column P concentration in the EPA, especially in areas adjacent to inflow structures and canals. However, unlike the results stated for the EPH model, the EWQM shows that decreasing EAA basin discharge P concentrations from 50 µg/L to 10 µg/L can significantly reduce P concentrations entering the Park through the S12 structures (**Figure 3-27**). Differences in the EPH and the EWQM are most likely due to differences in the way cells are sized and canals are simulated, but it is also not clear what STA input datasets were used by the EPH model (only one was shown for STA-3/4) and how long model scenarios were simulated into the future. Because output from the two models are not directly comparable at this time, a comprehensive comparison of EPH model and EWQM results, using identical input datasets and simulation run times is recommended.

Sawgrass-Cattail Model

The SAWCAT model (Wu et al., 1997), a probability model developed to understand the impact of soil P on cattail invasion in WCA-2A, found that the probabilities of sawgrass changing to cattail between 1973 and 1991 were most dependent upon the proximity of existing cattail stands and the spatial pattern of soil TP. A logistic function, built from spatial correlations of soil TP (DeBusk et al., 1994) and cattail distributions in WCA-2A (Jensen et al., 1995), estimated that the threshold for accelerated cattail invasion was ~650 mg/kg soil TP. The distribution of cattail stands was determined from spatial analysis of the

WCA-2A remote sensing data (Jensen et al., 1995). Although these data overestimate cattail invasion rates, general trends and dependencies of cattail on soil TP and the characteristics of neighboring vegetation stands did not change significantly when more accurate estimates of cattail cover based on aerial photography (Rutchey and Vilchek, in press) were used in later models (i.e., the ELVM described below).

Everglades Phosphorus Gradient Model

The EPGM was developed by private consultants for the Federal Government and was used by the District to determine if implementing the hydropattern restoration features of STAs would change the extent of cattail communities in receiving waters. The EPGM uses a first order settling mechanism for the transfer of phosphorus from the water-column to the sediments. Cattail densities are then predicted as a function of soil P concentrations. Because the EPGM assumes idealized flow patterns (uniform sheet flow), and because simulations are performed for average hydrologic conditions, the model only provides general indications of temporal and spatial scales of impact, and is not intended to predict water quality, quantity, and ecological conditions at any particular place or time. The EPGM has been calibrated for water quality and cattail growth in WCA-2A. Modeling assumptions and details of EPGM structure and performance are documented in Walker and Kadlec (1996).

Everglades Landscape Vegetation Model

The ELVM is being developed to study the mechanisms associated with macrophyte succession in order: (1) to understand and simulate vegetation dynamics in response to hydrology (from the SFWMM), available soil nutrients, and disturbances such as fire, hurricanes, and freezes; and (2) to provide a tool for evaluating various scenarios of hydrological and phosphorus reduction toward restoration of the Everglades. The ELVM simulates life cycles of each major plant community in a cell. There are several communities in a cell, which means that a cell is not treated as homogenous. Disturbances such as fire, hurricanes, and freeze are simulated based on historical frequencies. As a fire, hurricane, or freeze occurs, the model simulates its spreading rate, direction, and damage to each vegetation type in the landscape.

The ELVM can simulate the vegetation succession in WCA-2A for 62 years from 1995 to 2057 under different management scenarios. Theoretically, if agricultural runoff P was set to zero, preliminary ELVM results suggest that cattails will continue to increase for the next 20 years. The peak abundance reached depends on the depletion rate of soil P. This empirical depletion rate is an estimate of the removal of bioavailable P from the system through burial, incorporation into plant biomass, or export. With a high depletion rate, the potential cattail distribution in the WCA-2A landscape (43,300 total ha) could be 11,000 ha in 20 years. If the depletion rate is low, cattails could occupy as much as 17,000 ha in WCA-2A. The model also suggests that without taking any measures to reduce soil TP in WCA-2A, cattails will continue to occupy a substantial area of the landscape for several decades.

Everglades Landscape Model

The ELM, in the version that was applied to WCA-2A at a 0.25 km² grid cell scale, showed that it is likely that the ecosystem will maintain a eutrophic status for approximately a decade, even after external P loads have returned to normal levels (Fitz & Sklar, in press). This model currently is being used to indicate the extent to which periphyton communities may recover under low P-loading conditions. This recovery was found to be hindered in areas that were eutrophic and supported high macrophyte biomass.

Largely due to existing high soil nutrient concentrations and internal nutrient cycling, the eutrophic macrophyte habitats are likely to be maintained, and/or expand to some extent, even in the absence of high external P loads. There are uncertainties noted in this chapter concerning the understanding of all the ecological processes driving the Everglades, and these sources of error are important to consider in interpreting model results. However, model calibration and sensitivity analyses indicated that the ELM effectively depicted the ecosystem dynamics within the Everglades landscape (Fitz & Sklar, in press). As a tool for ecosystem analysis, the ELM is now being applied to the entire natural system of the Everglades, including the Conservation Areas, Big Cypress, and the Park.

Current Understanding, Critical Knowledge Gaps and Future Research Needs

The Everglades ecosystem developed under conditions of extreme P limitation, and it is clear that anthropogenic P loads have altered this unique resource. As described here, the results of experimental studies and measurements conducted along P gradients have increased our understanding of the progression of ecological responses to P enrichment in the Everglades. This information will serve as the basis for determining the concentrations and loads that cause these various responses. Available evidence indicates the following:

- The Everglades marsh is extremely sensitive to P enrichment, although the ecological changes caused by enrichment manifest themselves over different time scales ranging from days and weeks (e.g., microbial and periphyton changes) to several years or decades (e.g., vegetation changes such as cattail expansion).
- Changes in natural populations of Everglades flora and fauna (i.e., microbes, periphyton, vegetation, and invertebrates) have been documented in areas of the marsh where water-column TP concentrations exceed background levels of approximately 10 µg/L.
- Although natural populations of flora and fauna respond to P enrichment at different rates, most of these changes ultimately occur within a relatively narrow range of water-column TP concentrations between approximately 10 µg/L and 30 µg/L.
- These responses to P enrichment are consistent with eutrophication patterns that are well established for other freshwater ecosystems (e.g., Sawyer, 1947; Likens, 1972; Vollenweider, 1976; Harper, 1992).

Uncertainty remains over the extent of spatial and temporal variation in ecosystem responses to P enrichment and the rate of recovery following reductions in P inputs. Ongoing work by several research groups should help to address the issues described below.

Spatial Coverage of Sampling and Experimentation

The Everglades is a heterogeneous ecosystem at several spatial scales and previous research has not been distributed evenly among geographic regions or habitat types. Most studies have been conducted in WCA-2A due to accessibility and the presence of a pronounced enrichment gradient. Considerably less research has been conducted in the Refuge and the Park and no major field studies have been conducted in

WCA-3A. Field dosing studies have focused largely on slough and wet prairie habitats (Scheidt et al., 1989; Richardson et al., 1995; McCormick & O'Dell, 1996; Richardson et al., 1997; McCormick & Scinto, in press). Information on the response of sawgrass stands to P enrichment has come largely from observational studies (but see experimental findings from Craft et al., 1995; Miao & DeBusk, in press), and little is known concerning the response of marl prairies, which cover large areas of the southern Everglades and represent some of the most oligotrophic habitats in the ecosystem.

A largely untested hypothesis is that different habitat types may vary in their sensitivity to P enrichment. Evidence from the Everglades and from other ecosystems indicates that the persistence of natural populations of flora and fauna are linked closely to the heterogeneous nature of the Everglades landscape (synthesized in Davis & Ogden, 1994). Maintenance of this habitat mosaic requires that the most sensitive habitat types be protected from human disturbances such as P enrichment that drive the system towards spatial homogeneity (e.g., cattail expansion).

Temporal Patterns of P Accumulation and Ecological Responses

Intensive research over the last few years provides a reasonably good basis for predicting the progression of marsh responses to eutrophication. However, differences in the rate and extent of response to different P loading rates are still poorly understood. Ongoing experimental studies being conducted by various research groups have provided valuable insight into responses over short time periods (e.g., several years). However, given the short-term nature of most experimentation, such studies provide limited evidence for long-term changes (i.e. decades) that are of interest to water managers and regulators. Monitoring along marsh enrichment gradients provide the best available evidence of the long-term impacts caused by different P loads, even though conditions are less controlled and loads and concentrations may vary over time. Correlative relationships between marsh P concentrations and ecological change, when combined with controlled experimentation to support cause-effect relationships, provide the best available evidence for identifying P concentrations and loads that produce a long-term imbalance in Everglades flora or fauna.

Interactions Between P Enrichment and Other Natural and Anthropogenic Factors

Both natural (e.g., droughts, fires) and human-induced (e.g., altered hydroperiods and water depths) disturbances can affect ecological patterns in the Everglades, sometimes in a manner that may be similar to the effects of anthropogenic P loading (e.g., Newman et al., 1998). Interactions between these disturbances and increased P loading may intensify or, in certain cases, counteract the effects of P enrichment alone. Similarly, inputs of other nutrients such as N may intensify the effects of P enrichment in highly enriched areas of the marsh. Field and greenhouse experiments currently are underway to identify the significance of interactions between these environmental variables in order to improve our ability to predict ecological responses to multiple management actions (e.g., reduced P loads combined with hydropattern changes).

Hydrologic fluctuations and periodic fires, factors believed to influence ecosystem responses to P enrichment, have been important forces shaping the Everglades throughout the existence of this ecosystem (Davis, 1994). While these factors may alter the rate of ecosystem response to P enrichment, there is little evidence to suggest that human-induced changes in water depth or fire frequency determine the ecological changes that ultimately occur in areas of the marsh receiving external P loads.

Rates of Marsh Recovery Following Reductions in P Loads

Most emphasis has been on documenting the ecological impacts caused by P enrichment and the P concentrations and loads that cause various changes in the Everglades. An understanding of the rate of ecosystem recovery following load reductions is required to develop realistic timeframes and expectations for restoration. Key questions related to recovery include but are not limited to the following:

- How fast will water-column and soil P concentrations decline in enriched areas of the marsh following P load reductions?
- Will P and associated ecological changes (e.g., cattail expansion into sloughs) continue to spread across the marsh as a result of internal P loading even after external loads are reduced?
- How quickly will P-impacted areas of the marsh recover and what level of recovery can be expected?

Evidence from other ecosystems indicates that the rate of ecosystem recovery from eutrophication is considerably slower than the initial enrichment process (Perry & Vanderklein, 1996). Field and greenhouse studies have been initiated to address recovery issues. In addition, cessation of dosing in field mesocosm and flume studies followed by continued monitoring in these experimental systems should provide useful data for predicting recovery rates in areas of the marsh already impacted by P enrichment.

Findings on Ecological Needs

- The Everglades ecosystem was naturally unenriched (oligotrophic) and phosphorus inputs came primarily from the atmosphere.
- Ecosystem function and biological diversity were based on low-nutrient conditions in the Everglades, including those leading to higher levels of the food web, such as wading birds.
- Canal inflows have become a major source of surface water P to the EPA, with the greatest increase in the northern Everglades.
- Controlled dosing studies combined with sampling along marsh P gradients in WCA-2A indicate that species changes begin to occur at water-column TP concentrations of about 10 parts per billion.
- Phosphorus enrichment leads to a decline in the coverage of sawgrass, sloughs and wet prairies and these habitats are gradually replaced by cattail.
- Phosphorus loads have altered the Everglades resource. Ecological changes caused by enrichment are manifest over several time scales. Changes generally begin to occur in areas of WCA-2A at water-column TP concentrations ranging between roughly 10 and 20 ppb. This response range is similar to those established previously for other types of freshwater ecosystems.
- Evidence from other ecosystems and modeling suggests that the rate at which the Everglades ecosystem recovers from eutrophication will be considerably slower than the initial enrichment process.

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